EFFECTS OF PERMAFROST THAW ON NITROGEN AVAILABILITY AND PLANT SOIL INTERACTION IN A BOREAL ALASKA LOWLAND

By

Rebecca Anne Finger

RECOMMENDED:

Knut Kielland Ph.D.
Advisory Committee Member

Roger Ruess Ph.D.
Advisory Committee Member

Merritt Turetsky Ph.D.
Advisory Committee Co-Chair

Eugenie Euskirchen Ph.D.
Advisory Committee Co-Chair

Diane Wagner Ph.D.
Chair, Department of Biology and Wildlife

APPROVED:

Paul Layer Ph.D.
Dean, College of Natural Science and Mathematics

John Eichelberger Ph.D.
Dean of the Graduate School

12/8/14
Date

EFFECTS OF PERMAFROST THAW ON NITROGEN AVAILABILITY AND PLANT SOIL INTERACTION IN A BOREAL ALASKA LOWLAND

A

THESIS

Presented to the Faculty

of the University of Alaska Fairbanks

in Partial Fulfillment of the Requirements

for the Degree of

MASTER OF SCIENCE

By

Rebecca Anne Finger, B.S.

Fairbanks, AK

December 2014

Abstract

Permafrost thaw in boreal peatlands causes an ecosystem state change as black spruce forests with permafrost transition into saturated, non-forested collapse scar bogs or fens. Previous studies have suggested that permafrost thaw can increase soil nitrogen (N) bioavailability. However, it is unclear whether these changes in N availability are directly related to changes in N pools or mineralization rates in surface soils (active layer dynamics), or whether increasing N can be attributed to N mobilization from thawing permafrost soil organic matter at depth. I examined plant species composition and aspects of N cycling along triplicate permafrost-thaw gradients in interior Alaskan peatlands. Each gradient comprised plots situated in a 1) forested plateau with intact permafrost (hereafter called permafrost forest) 2) forest experiencing active thaw (drunken forest), 3) moat representing initial stages of complete thaw (moat), and 4) collapse scar bog representing post-thaw succession following complete permafrost thaw (collapse bog). I found that both organic and inorganic N concentrations in soil solution increased with thaw. Drunken forests with active permafrost thaw had the greatest mean concentrations of total dissolved N relative to the other gradient plots. Elevated levels of dissolved N in the drunken forest plots were due primarily to high concentrations of large molecular DON. The moat and collapse scar bog plots had greater inorganic N concentrations on average than the permafrost forest or the drunken forest, suggesting that changes in plant-available N do not occur immediately upon thaw, but are influenced by vegetation or soil succession occurring decades to centuries after thaw is initiated. However, across all of the community types, I found that deeper soil horizons corresponded to greater concentrations of DIN and DON when thaw was deepest (September), suggesting that permafrost soil horizons are playing a role in changing N availability post-thaw. Vegetation responses to permafrost thaw included changes in plant community composition, deeper rooting profiles, and changes in foliar N and $\delta^{15}N$ values. Plant foliar and litterfall N concentrations increased with collapse bog succession and showed relationships with concentrations of DIN, suggesting that plants are utilizing additional mineralized N. Together, my results suggest that the conversion of lowland permafrost forests to collapse scar bogs increases N availability both by increasing turnover of the permafrost organic matter pool as well as through longer-term successional processes. At least some plants are able to capitalize on "new" sources of N available post-thaw, but it is

unclear from my results whether plants are able to acquire N mobilized by thawing permafrost organic matter deeper in soil profiles.

Table of Contents

Page

Page

List of Figures

Page

Page

List of Tables

Page

Acknowledgments

Without the support, encouragement, and advice of my co-advisors, Eugenie Euskirchen and Merritt Turetsky, this thesis would not have been possible. Thank you for encouraging me to get creative and challenge myself in order to tell a good scientific story. I would also like to thank my committee members, Roger Ruess and Knut Kielland, for conceptual diagrams on white boards, support, insight and feedback, and occasionally making fun of me. In addition to the invaluable advice and guidance from my committee, I am gratefully for the numerous helpers in both the field and laboratory including: Colin Edgar, Jesse Barta, Carolyn Gibbs, Carmel Johnson, Lily Cohen, Jim Lokken, Lola Oliver, Karl Olsen, and Ben Abbott. Research funding support was provided by the National Science Foundation, Center for Global Change at the University of Alaska Fairbanks, and the Society of Wetland Scientists.

Finally, I would like to thank my friends and family for the love and support they have shown me over the last few years. I am sure you all know way more about permafrost, *Sphagnum*, and boreal nitrogen cycling than you ever thought you would need to know. Sometimes it takes a village (or coffee, falafel, and the occasional ski trip) to survive graduate school. Thanks!

Chapter 1: Introduction

1.1 Permafrost thaw in peatlands

Many boreal and subarctic peatlands are controlled by permafrost degradation-aggradation cycles that shape and define regional hydrology (O'Donnell *et al*. 2011; Quinton & Baltzer 2012), biogeochemistry (Jones 2005; Keuper *et al.* 2012), and plant community structure (Beilman 2001; Jorgenson *et al.* 2001; Zoltai 1993). The degradation-aggradation cycle often takes approximately 600 years and is largely controlled by disturbance events that trigger thaw as well as the slow accumulation of insulating peat layers that ultimately allow permafrost to return (Zoltai 1993). However since the mid-1800s, warmer climate conditions have caused widespread permafrost thaw across the discontinuous permafrost zone (Chapin *et al*. 2010; Osterkamp *et al.* 2009), and it is still unknown whether projected warming will make ecological conditions unsuitable for permafrost aggradation. Currently, mean annual near-surface permafrost temperatures are within 1 or 2° C of thaw throughout the boreal forest, making permafrost highly susceptible to degradation (Camill 2005; Osterkamp *et al*. 2000). Therefore, much of the boreal forest region may become too warm to support permafrost under future climate scenarios, with consequences for forest distribution, vegetation community structure, and biogeochemical cycling (Jorgenson *et al*. 2001; Turetsky *et al.* 2007).

Approximately 25% of the discontinuous permafrost zone of interior Alaska consists of peaty-silty lowlands (Jorgenson *et al*. 2013). In these lowland sites, slow-growing black spruce (*Picea mariana*) is found atop thick organic layers. Permafrost generally develops in these thick, insulating peat layers, and form raised peat plateaus (Harris *et al.* 1988). However, fractures in the peat mats can expose cold soils to increased thermal radiation and cause permafrost to degrade (Camill 2005). Thawed sites often subside between 1 to 2 m from the original permafrost plateau and destabilize the forest canopy (Beilman 2001; Camill 1999). Because permafrost thaw leads to a physical displacement of the forest floor, this slumped, uneven topography is often referred to as thermokarst. Thermokarst development typically is limited to ice-rich soil conditions, which often are found in low-lying areas with fine-grained deposits and poor soil drainage (Jorgenson *et al.* 2001). In thermokarst features, forests are drowned by newly formed moats of collected water. Thick organic floating mats rapidly develop within a decade of initial thaw, supporting hydrophilic plant communities of sedges, such as *Carex aquatalis*, and

mosses such as *Sphagnum riparium*. The development of a ground layer dominated by *Sphagnum* enhances water storage in surface soils and slows down decomposition and nutrient cycling. Over time, peat accumulates above the water table, and drying associated with this autogenic succession allows for the colonization of more dry-adapted species including small shrubs and trees with deeper rooting profiles and hummock-building mosses (Camill 1999).

1.2 Plant nitrogen economies

Nitrogen (N) and phosphorus (P) limitations often result in low levels of both plant growth and soil organic matter decomposition (Chapin 1980), favoring species with conservative nutrient use (Granath *et al.* 2010; Sorrell *et al.* 2011), mycorrhizal associations (Hobbie *et a.* 2009; Inselsbacher & Näsholm 2012) and organic nitrogen uptake (Nasholm *et al*. 1998; Jones & Kielland 2002; Kielland *et al.* 2007; Schimel & Bennett 2004). Many plants in nutrient poor systems, like the boreal forest, adapt to low N supply by increased resorption of foliar nitrogen during senescence and retention in evergreen tissues, woody biomass, rhizomes and roots for the next growing season (Aerts 1996). When nutrients are resorbed, plant litter quality generally decreases, which slows decomposition and soil microbial processes (Aerts *et al.* 1999). Conversely as nutrient supply increases, plants are presented with several options for utilizing additional N supplies, including increasing production, increasing tissue nutrient concentrations, or decreasing tissue life spans (Aerts & Chapin 2000; Berendse & Aerts 1987). Therefore relative changes in common plant-nutrient indicators such as growing season foliar nutrient concentrations, litterfall nutrient concentrations, and nutrient resorption efficiencies can often help elucidate patterns in plant N use and overall nutrient limitations (Sorrell *et al.* 2011). Ericoid and ectomycorrhizal (ECM) fungi can also increase vegetation nutrient access in nutrient-limited systems. Mycorrhizal fungi assist their symbiotic host plants by increasing root surface area, directly transferring N to their host-partner plant (Hobbie *et al.* 2009), or by producing enzymes that break down complex organic molecules to release into free amino acids that are available for plant uptake (Jones & Kielland 2002). Once released into the soil, amino acids can often be directly used by both plants and microbes (Kielland *et al.* 2007; McFarland *et al.* 2010); making free amino acids an important component to soil nutrient supplies.

The presence of permafrost is characteristic of cold and wet soil conditions, which inhibit microbial activity and contribute to nutrient limitations, such as N and P, to primary productivity and decomposition (Van Cleve *et al.* 1981; Van Cleve *et al.* 1983). Plants with lower nutrient requirements, such as *Sphagnum* and evergreen ericaceous shrubs, typically dominate the understory communities of lowland permafrost forest (Granath *et al*. 2012). Specialized adaptations to utilize organic N supplies, either through direct uptake or through mycorrhizal associations, allow lowland permafrost forest species to establish and grow, albeit slowly, in cold and shallow soils. However, during permafrost thaw, soil disturbance and saturation of the rhizosphere often changes species composition which has repercussions for mycorrhizal ecology and alter how plants acquire nutrients. Warming of soils may stimulate N mineralization both in deeper permafrost organic matter soils as well as in the shallow active layer soils (Natali *et al.* 2012; Weedon *et al.* 2012). Recent studies suggest that thawed permafrost organic matter can act as a source of plant-available N (Keuper *et al.* 2012; Schurr *et al.* 2007), but it remains unclear whether plants are able to access and utilize deeper sources of N in post-thaw sites, where saturated soil conditions with low redox potential may further impede mineralization and exacerbate N availability over longer time periods. Therefore, if there are substantial N inputs from thawed permafrost organic matter, are plants able to utilize these sources deeper in the soil profile? Or is plant uptake of these deeper N sources limited by access and/or the anoxic soil conditions that typically form in thermokarst features such as collapse scar bogs?

The objectives of this study were to examine how N availability, plant community structure, and plant N use are affected by permafrost thaw (Figure 1.1). Preliminary results of plant foliage from lowland boreal permafrost forests and permafrost thaw features have indicated that these ecosystems have high P concentrations and low N:P (Figure 1.2), indicating N limitation across these systems. Therefore, in light of these early findings, I tested two hypotheses regarding N cycling along permafrost thaw gradients extending from a permafrost forest to a thaw margin to a collapse scar bog:

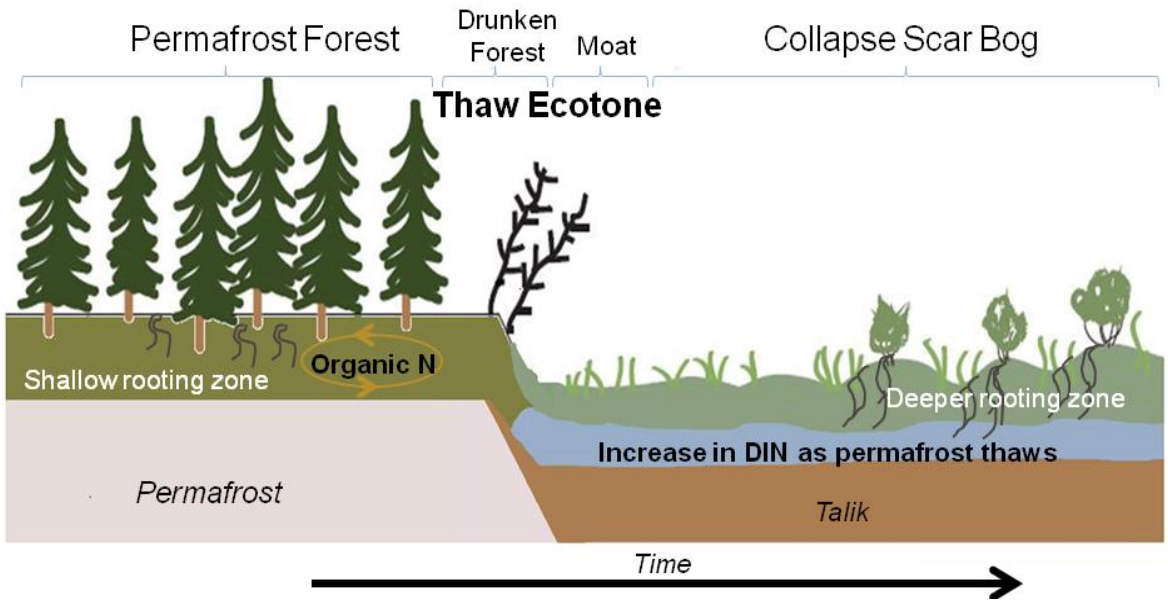

Figure 1.1: Conceptual framework examining changes in nitrogen dynamics and plant-soil interactions along a thaw gradient. As permafrost thaws, DIN sources are predicted to increase resulting in changes to plant foliar chemistry, rooting stratigraphy, and mycorrhizal associations. Within the drunken forest, permafrost is actively thawing, while moat sites form within one decade of thaw. The collapse scar bog is likely within 100-300 years post thaw (Klapstein *et al.* 2014).

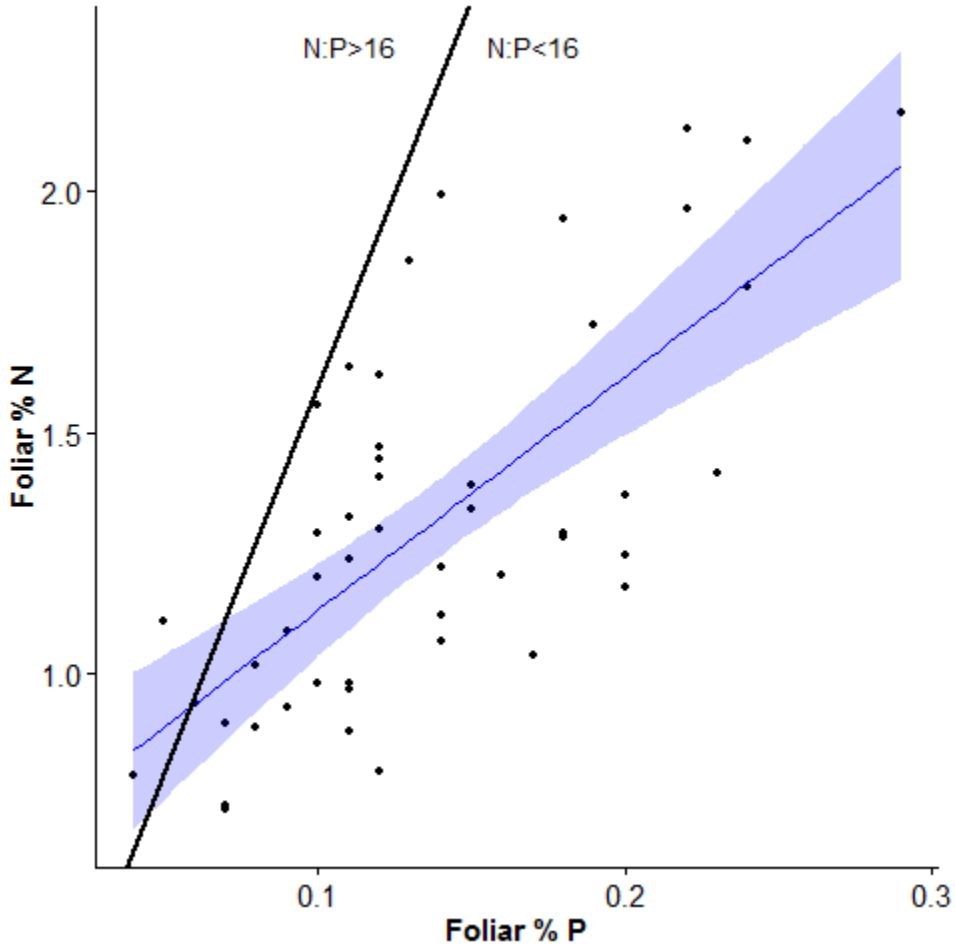

Figure 1.2: Relationship between foliar N and P concentrations from 49 samples from APEX boreal lowlands experiencing ongoing permafrost thaw, collected during the summer of 2013. N:P≥16 indicates plants are P limited while N:P<16 are indicative of plants that are either N limited or N and P co-limited (Güsewell & Koerselman, 2002). Blue line and blue shading represent a linear model regression and confidence band respectively of the scatterplot data.

(1) Permafrost thaw increases dissolved inorganic N (DIN) pore water concentrations due to increased turnover in both active layer and permafrost soil organic matter (SOM). I predicted that there would be low concentrations of pore water DIN in lowland permafrost forest soils, but that as permafrost thaws pore water DIN concentrations will steadily increase. As active layer depth increases and soil temperatures increase, warmer, shallower soils were predicted to see larger concentrations of DIN. I also expected higher concentrations of DIN with depth, especially in ecotonal community types undergoing active permafrost thaw where historic permafrost SOM is actively released into the system. Collapse scar bogs were predicted to have intermediate levels of pore water DIN due to saturated soil conditions constricting microbial mineralization and decomposition, coupled with peat accumulation contributing to N immobilization and limitation.

(2) Thaw-mediated changes in N availability will be associated with changes in vegetation community composition and plant nutrient-use strategies. I predicted that as permafrost thaws and N availability increases, plants that are adapted to low N environments, such as evergreen shrubs and *Sphagnum*, will be replaced by faster growing species that are better adapted to utilize more abundant N sources, such as sedges and deciduous shrubs. I also predicted rooting depths would increase with permafrost thaw as a response to an increase soil temperatures and N mineralization at depth from released permafrost SOM, with deeper rooting plants located in collapse scar bogs. Foliar and litterfall N were also predicted to increase with thaw, as rooting depths and N availability changes, and to be positively related to pore water DIN concentrations. Conversely, I expected that resorption efficiency (RE) would decline following thaw as a result of increasing N availability. I also predicted that $\delta^{15}N$ values would be more depleted in the permafrost forest due to mycorrhizal partitioning (Hobbie & Hobbie 2006), and enriched in the collapse scar bog due to increasing N availability. This increase in $\delta^{15}N$ enrichment was predicted to increase with rooting depth as plants accessed older (and more enriched, sensu Kohzu *et al.* 2003) sources of thawed permafrost organic matter.

Chapter 2: Study Site

Research was conducted in conjunction with the Bonanza Creek Long Term Ecological Research (BNZ LTER) program and the Alaskan Peatland Experiment (APEX) adjacent to the

Tanana River floodplain approximately 35 km southeast of Fairbanks, AK (64.82º N, 147.87º W). The study area was established in 2008 to gain a better understanding of the interactions between collapse scar bog development and atmospheric-terrestrial carbon cycling (Euskirchen *et al.* 2014; Klapstein *et al.* 2014). In this region, air temperatures change dramatically across seasons, ranging from -50°C in January to +33°C in July with a mean annual temperature around -2.9°C (1988-2014; BNZ LTER weather data). Atmospheric N deposition is low relative to many regions in the world, averaging around 0.2 kg N ha^{-1} y^{-1} (Jones 2005). Growing seasons are short, averaging approximatly135 days, resulting in cold soil temperatures. Moderately ice-rich and discontinuous permafrost is found in low-lying, poorly drained areas. Such areas have sparse black spruce with an average tree density of <800 trees per hectare (Churchill 2011).

Throughout the last few hundred years, several collapse scar bogs have developed within the larger lowland permafrost forest within the vicinity of APEX thermokarst sites (Klapstein *et al.* 2014). Along active permafrost degradation margins, there is approximately 0.5-1 m of ground subsistence, creating a slump in the topography of the landscape. Following this ground subsidence, soils saturate and collapse scar bogs develop. Trees tilt and eventually die along the thaw margins due to soil destabilization and flooding, thereby creating "drunken forests" which eventually fall into the expanding collapse scar bog and are buried by post-thaw accumulation of moss and peat.

Due to increases in light, nutrients, and soil moisture, the post-thaw community is dominated by fast-growing aquatic plant species such as sedges and hydrophilic *Sphagnum* mosses. Over time, a floating mat (approximately 60 cm thick) of peat develops above approximately 50 cm of standing water. Largely as a result of autogenic wetland succession, hummock-hollow microtopography develops with woody plants such as leather leaf (*Chamaedaphne calyculata)*, dwarf and bog birch (*Betula nana and B. glandulosa*), larch (*Larix laricinia*) and black spruce emerging in larger, drier hummocks. Hollows remain saturated and close to the water table with more hydrophilic vegetation.

Chapter 3: Methods

3.1 Sampling design

Three separate forest-collapse scar bog systems were selected to examine plant community composition, N availability, and plant N acquisition strategies. Transects were selected so that bogs were hydrologically separate, due to the heterogeneity of the permafrost forest-collapse scar system. Each transect comprised four different plant community types: a forested permafrost peat plateau (Forest), an adjacent ecotone experiencing active permafrost degradation (including a drunken forest and a saturated moat, herein referred to as Drunken Forest and Moat respectively), and a collapse scar bog (Bog) where permafrost has completely degraded (Klapstein *et al*. 2014). The study design utilized a space for time substitution that allowed for the examination of the impacts of permafrost thaw on decadal to century time scales, with Drunken Forest and Moat sites representing annual to decadal time scales, and collapse scar bogs representing 50-100+ years post permafrost thaw ecological succession (M. Jones *unpublished data*). Within 5 m of the established transects, four 1 m^2 plots were haphazardly selected within the forest and bog community types for vegetative and soil analyses. Due to size limitations within the narrow bands comprising the ecotonal community types, only three 1 m^2 plots were randomly selected within each of the drunken forest and moat communities for additional analyses.

3.2 Plant community composition and environmental variability along the gradient

To survey changes in understory plant community composition, percent cover data were collected for each community type along each transect. A 0.5 × 0.5 m frame was used at each sampling plot for a visual assessment of percent cover for nonvascular and subcanopy vascular vegetation (plants found up to 1 m above the moss surface), using nomenclature from the USDA PLANTS Database (http://plants.usda.gov, 7 July 2014). For vascular plants, total cover for each plant species was estimated and assigned to a plant functional group: grass, sedge, herbaceous forb, deciduous shrub, evergreen shrub, or tree (Table A-1). Four ground cover functional types were used for nonvascular plots: plant litter, lichen (includes fungi), *Sphagnum*, and true moss (i.e. feather moss, *dicranum* species, etc.). The mathematical mean of percent cover data across

plots within each community type and transect was used to characterize landscape-level community compositions.

Environmental variables, including soil temperature at 10 cm depth, soil volumetric moisture content at 10 cm depth, and seasonal ice depth, were also recorded during each pore water sampling event throughout the growing season at each sampling plot. Soil temperature was measured using a 10 cm probe thermometer that was manually inserted into the soil at each sampling plot. Soil moisture was also measured manually using a ThetaProbe soil moisture sensor (Delta-T Devices, Cambridge, England) inserted 10 cm vertically into the soil surface. Seasonal ice depth was measured using a 1.5 m long tile probe. If no ice was encountered upon complete insertion of the tile probe into the ground, then sites were considered to be completely thawed.

3.3 Rooting depth and root abundance index

Rooting depth and relative root abundance were measured using soil cores collected in late July and early August of 2013. Soil cores were collected using a 5 cm diameter metal core barrel adjacent to each 1 m^2 sampling plot along the three transects. Core depth was dependent on active layer depth and floating peat mat, and generally correlated to the maximum depth of the nearby lysimeter assembly (see below), with forest cores at 30 cm depths, and thaw ecotone and bog core depths collected at 45-60 cm below the surface. Once excavated, cores were divided into 5 cm increments and placed on ice to be brought to the laboratory.

Each 5 cm core increment was visually inspected for up to 10 minutes and then given a root abundance score based on the number of apparent live roots and the size of the roots found in that increment (Harden *personal communication*). Root relative size was classified by root diameter and divided into four categories: very fine (<1 mm), fine (1-5 mm), medium (5-10 mm), and coarse (>10 mm). The number of roots within a size class was then approximated and given an abundance index score where few (<10 roots) was assigned an index of 10, common (10-100 roots) was assigned an index of 20, and many (<100 roots) was assigned an index of 30. Indices for each size class per core increment were then added together for the total root abundance score for that soil increment.

3.4 Pore water nitrogen concentrations along rooting profiles

Soil pore water samples were collected as an index of temporal fluxes of biologically available nitrogen across rooting zones and depths throughout the field season. In mid-June 2013, 10 cm microlysimeter Rhizon SMS moisture samplers (Eijkelkamp Agrisearch Equipment, the Netherlands) were installed within each 1 m^2 plot along the three transects. Before insertion into the soil, each Rhizon sampler was taped to a 60 cm piece of PVC pipe in order to insert samplers at desired depth intervals: 5-15 cm, 20-30 cm, and 50- 60 cm. However, due to the permafrost table in the forest at an average depth of around 40 cm, 30 cm PVC pipes were used for all forested sites and samplers were buried at 5-15 cm and 20-30 cm depths. Using a hand drill to pass through seasonal ice, 2.5 cm diameter holes were drilled into the soil at each sampling plot in the forested sites. PVC pipes were then inserted into pre-drilled holes until the top of the pipe was flush with the ground surface to insure proper Rhizon placement. Rhizons were left in place for two weeks prior to the first collection to allow for equilibration in the soil column.

Soil pore water samples were collected every three to four weeks from late June to late September, 2013 for a total of five sampling events. However, the presence of seasonal ice and arid soil conditions periodically limited some soil pore water sample collection through the growing season. Prior to sampling for chemical analysis, a small amount of pore water was suctioned into a 20 mL syringe and used as a prerinse for the Rhizon, syringe, and sampling bottle to remove sampler tubing head space and mitigate contamination. Because the Rhizon samplers have a 1 μm pore size membrane, no additional filtration was required prior to collection. Between 10-20 mL of soil pore water sample was extracted by syringe and ejected into acid-rinsed bottles. After extraction, samples were placed on ice packs in a cooler and brought to the laboratory. Samples were then split into three parts for three different analyses: (1) 5 mL was added to 20 mL of deionized water and analyzed for total dissolved nitrogen (TDN), (2) 5 mL was refrigerated prior to NO_3^- and NH_4^+ analysis (dissolved inorganic nitrogen; DIN), and (3) 0.5 mL was frozen at -20°C to await amino acid analysis. Samples for TDN were run with a TOC-V Analyzer with the TDN module (Shimadzu Scientific Instruments, Columbia, MD USA). DIN samples were analyzed using a Technicon II Autoanalyzer ($NH_4^+ + NO_3^-$) (Whitledge *et al.* 1981). Dissolved organic N (DON) was then determined as the difference

between TDN and DIN concentrations. Amino acids were analyzed using a modified ninhydrin reaction (Rosen 1957). Absorbance at 570 nm was measured on a Perkin-Elmer UV/Vis Lambda 25 spectrometer. Amino acid concentrations were determined by comparison to a leucine standard analyzed at the same time as the soil samples.

3.5 Plant foliar chemistry, nitrogen-resorption efficiency, and stable isotope analysis

Harvested plants of dominant functional types were used to quantify aboveground carbon and nitrogen concentrations. Plant biomass was collected in late July 2013 to coincide with peak seasonal biomass production in order to estimate nutrient pool sizes. Three plots from each transect's four community types were designated for biomass sampling. Using a 20 cm × 20 cm frame placed adjacent to the lysimeter plots, vascular vegetation was removed down to the moss surface. Biomass was then brought to the lab and subdivided into leaves, stems, and litterfall. For nonvascular plants, the top 3 cm was collected. All harvested and sorted tissues, mosses, and litter samples were dried at 60° C for 3 days and weighed. Plant tissues were then ground using a ball-mill, packed into combustion tins, and analyzed for percent C and N on an elemental analyzer COSTECH ECS 4010 CHNS-O analyzer (Costech Analytical Technologies Inc., Valencia, CA, USA). The mean of plant biomass and elemental composition per tissue type and species at each community type and transect was used for estimations of carbon and nitrogen contents at the ecosystem level (mg m^{-2}) and vegetation C:N ratios.

Based on the dominate understory plant species in the plant community survey described above, one species, *Chamaedaphne calyculata,* was observed across all four community types. This species was used to estimate plant foliage chemistry and plant nitrogen-resorption efficiency, as indicators of nitrogen use and acquisition strategies. *C. calyculata* is an ericaceous evergreen shrub, associated with ericoid mycorrhizae, and often found in nutrient-limited ecosystems (Bartsch 1994). Previous fertilization studies have shown that *C. calyculata* increases biomass, shoot lengths, and foliar N concentrations in response to increased nutrient availability, suggesting that this plant would likely be responsive to potential changes in soil N availability across our study gradient (Bartsch 1994; Bubier *et al.* 2011).

Leaf litter traps were placed underneath *C. calyculata* shrubs in early June and checked periodically throughout the season. Plants were revisited during periods of peak biomass in late-

July, and during senescence and leaf fall in late-September for green leaf foliage and litter collection, respectively. After collection, foliage samples and leaf litter were dried at 60 °C and ground for analysis of total N using a COSTECH ECS 4010 CHNS-O analyzer (Costech Analytical Technologies Inc., Valencia, CA, USA). Nutrient-resorption efficiency (RE) was then calculated as the change in foliar N pools between green and senescent leaves [$RE=(N_{Green}-N_{Senecsed})/N_{Green}$ x 100; Aerts *et al.* 1999].

Based on the plant community surveys described above, two additional species were found in two or more community types and have different mycorrhizal status. These species, *Carex aquatilis* (*C. aquatilis*) *and Betula glandulosa* (*B. glandulosa*), along with *C. calyculata*, were selected for stable isotope analysis. Green leaves were collected from all three species (found adjacent to survey plots), and brought to the lab for drying. Plant leaves were dried at 60 °C and ground using a ball mill to prepare for analysis. Prepared samples were sent to the University of Alaska Fairbanks Stable Isotope Facility for processing using a ratio mass spectrometer and combustion analyzer.

3.6 Statistical Analysis

Statistical tests and analyses were performed using R version 3.0.2 (R Development Core Team, 2013) in order to identify trends across the development of thermokarst collapse scar bogs in temporal pore water collection, root abundance indices, and vegetation chemical composition. Multiple regression models were not constructed for amino acids because earlier statistical analyses revealed that community type did not affect amino acid concentrations. Interaction terms were not included in final model construction as they did not significantly alter the slopes of the independent variable coefficients. Diagnostic plots and visual assessments were used to ensure no major statistical assumptions were violated with regards to residual homogeneity, independence, and normality. Statistical significance was assessed using $\alpha=0.05$. Linear regression and analysis of variance (ANOVA) tests, followed by Tukey HSD *post hoc* comparisons, were used to classify controls on relative root abundance, plant foliage chemistry and stable isotope abundance. Multiple regression models were used to predict nitrogen pore water concentration using environmental site characteristics and community types. Backwards

stepwise regression using Akaike information criteria (AIC) was then used to identify best fit model.

Due to an incomplete factorial design because forest pore water collection was limited by the permafrost table, and consequently did not include measurements at 60 cm in the forest, the pore water data had to be adjusted to allow for statistical interpretation. As a result, the data set was not of full rank and community type-by-depth interaction terms could not be initially evaluated. To solve this issue, all possible community type and depth combinations were combined to look at interactions on pore water N chemistry. Then, using stepwise procedures as outlined by Zuur *et al.*(2009) and Bolker *et al.*(2009), a generalized linear mixed effects model was constructed to assess N concentrations in pore water for DIN, DON, TDN, and free amino acids separately by date, community type, and depth. Mixed effects models were performed using the package 'nlme' in R (Pinheiro *et al*. 2014). To address repeated seasonal measurements at sampling plots a nested random factor of sampling date within plot ID was included as a random effect in the model. To reduce heterogeneity in the data, a multiple variance structure for transect location was added to the model to account for inter-transect variability across the study area. Fixed effects and possible interactions were determined using log likelihood ratio test. The final models for pore water N chemistry analyses designated community, lysimeter depth, and sampling date as fixed effects, and transect as nested random effects. Tukey HSD *post hoc* comparisons of means tests were conducted using the package 'multcomp'(Hothorn *et al.* 2008).

Predictions about major trends and shifts in vegetation composition across community types were evaluated through canonical correlation analysis (CCA) and multi-response permutation procedure (MRPP); both techniques using Sorenson (Bray-Curtis) dissimilarity measures within the program PC-ORD 5.31 (Kruskal & Wish 1978; McCune & Mefford 1999). The canonical correspondence analysis identifies community gradation by constraining an ordination of a matrix of plant percent cover data at each sampling plot by a matrix of plot-level environmental variables. Environmental variables included maximum seasonal ice depth, mean growing season soil moisture at 10 cm depth, mean growing season soil temperature at 10 cm depth, and modeled mean estimates for TDN, DON, and DIN concentrations for each sampling plot. The advantage of this technique is that both changes in species composition and environmental soil conditions are considered, which helps identify potential direct and indirect

effects of changing environmental conditions on vegetation along the permafrost-thaw gradient. Following visual inspection of the confined biplot ordination, I performed a MRPP for testing if there was an observed statistical difference between species composition in the different community types, independent of changing environmental conditions. Data were rank transformed during MRPP to provide data standardization (McCune & Mefford 1999).

Chapter 4: Results

4.1 Effects of permafrost thaw on soil conditions and dissolved N availability

Mean growing season soil temperature at 10 cm depth ($F_{[3,38]}$=32.89, p<0.001), volumetric moisture content within the top 10 cm ($F_{[3,38]}$=59.62, p<0.001), and maximum active layer depth ($F_{[3,38]}$=768.9, p<0.001; Table 4.1) varied along the thaw gradients. Soils were colder and drier in the permafrost forest than in the other community types. Among the communities affected by thaw, the warmest and wettest soils were found in the moat.

Concentrations of TDN, DIN, and DON varied among community types, depths, and sampling dates. Because TDN was predominately organic N, TDN and DON concentrations had very similar trends with regards to seasonal sampling (Figure 3.2b). Only TDN and DON concentrations had a clear sampling date x community type interaction (Table 4.2, Figure 4.a,b). When community types were averaged across sampling dates, TDN and DON concentrations in August were lower on average compared to the other sampling dates (p<0.001 for all post hoc contrasts). This is attributed to declining concentrations of soil solution N in the drunken forest, moat, and bog community types during the August sampling date (Figure 4.a,b). Amino acid concentrations averaged approximately half that of DIN, and also varied among sampling dates, with no community type x date interaction (Table 4.2), with the smallest concentrations observed across all gradient plots in September (Figure 3d).

Both TDN and DON concentrations exhibited a depth x sampling date interaction. Generally approximately 80-90% of TDN was DON. Averaged across community types, TDN concentrations varied with soil depth in during all sampling events, except for July 24 (Figure 3.2a). Depth interactions revealed greater concentrations of DON at depth compared to near surface concentrations in early July. Both TDN and DON concentrations also exhibited a

Table 4.1: Environmental characteristics for each community type along the thaw gradients. Data are growing season means ± one standard error. Letters indicate post-hoc test differences between community types.

Community Type	Dominant Species	Soil temperature (°C)	Soil moisture (% VMC)	Maximum seasonal thaw depth (cm)
Forest	*Picera mariana, Rhododendron* spp., *Vacciniumspp., Rubus chamamorus*, Feather moss spp., *Sphagnum* spp.	4.26 ± 0.25**a**	24.19 ± 3.54**a**	50.58 ± 1.91**a**
Collapse	*Carex* spp., *Eriophorum* spp., *Chamadaphne calyculata, Rubus chamamorus, Sphagnum* sp	6.11 ± 0.36**b**	53.11 ± 4.98**b**	70.28 ± 3.69**b**
Moat	*Carex* spp., *Eriophorum* spp., *Chamadaphnea calyculata, Andromea polifolia, Sphagnum riparium*	9.66 ± 0.57**c**	79.39 ± 2.34**c**	> 150 **c**
Bog	*Carex* spp., *Eriophorum* spp., *Chamadaphnea calyculata, Betula glandulosa, Larix laricina, Sphagnum* spp.	8.77 ± 0.52**c**	72.49 ± 1.92**c**	> 150 **c**

Table 4.2: Results of a three-way ANOVA analyzing the effects of community type, sampling date, sample depth, and two-way interactions on total dissolved N concentrations (TDN), dissolved organic N (DON), dissolved inorganic N (DIN), and amino acids. Degrees of freedom (df) are reported with numerator and denominator values.

Fixed effects	**TDN**		**DON**		**DIN**		**Amino Acids**	
Term	F (df)	P	F	P	F	P	F	P
Community type	**7.57** $_{3,99}$	**<.001**	**10.49** $_{3,99}$	**<.001**	**3.80** $_{3,99}$	**0.013**	0.44 $_{3,104}$	0.727
Date	**17.99** $_{3,239}$	**<.001**	**27.63** $_{3,239}$	**<.001**	**8.39** $_{3,239}$	**<.001**	**16.12** $_{3,259}$	**<.0001**
Depth	**5.022** $_{2,99}$	**0.008**	**5.07** $_{2,99}$	**<.001**	1.47 $_{2,99}$	0.234	1.35 $_{2,259}$	0.261
Community type x Depth	**4.39** $_{9,239}$	**<.001**	**3.54** $_{9,239}$	**<.001**	1.42 $_{9,239}$	0.180	1.13 $_{9,259}$	0.341
Community type x Date	**3.14** $_{10,94}$	**0.002**	**4.04** $_{10,94}$	**<.001**	1.51 $_{10,94}$	0.147	0.78 $_{10,269}$	0.649
Depth x Date	**6.21** $_{6,239}$	**<.001**	**4.73** $_{6,239}$	**<.001**	**7.58** $_{6,239}$	**<.001**	**2.22** $_{6,259}$	**0.041**

Random effects	Standard		Standard		Standard		Standard	
Term	deviation	Residual	deviation	Residual	deviation	Residual	deviation	Residual
Sample ID/Date	0.18	0.202	0.233	0.127	0.11	0.102	0.041	0.039

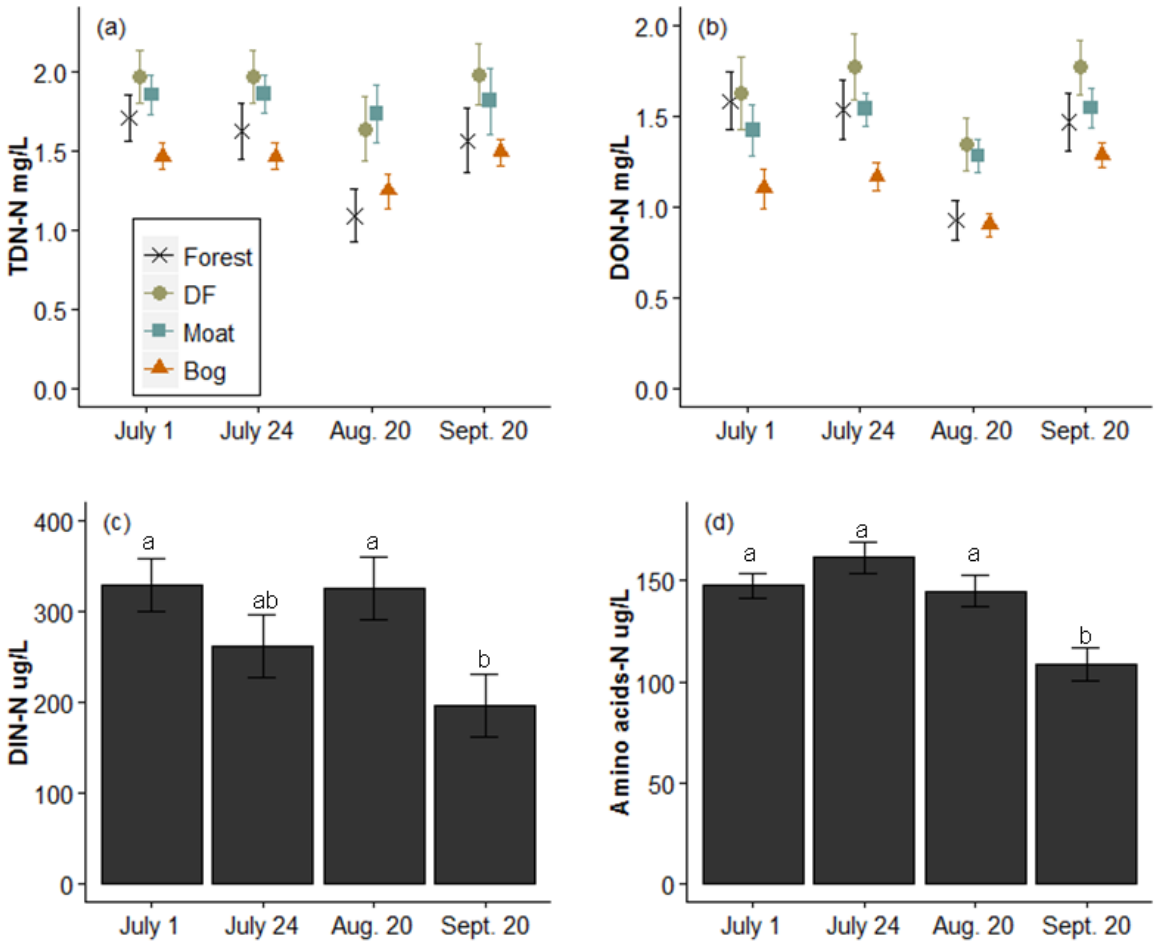

Figure 4.1: Seasonal changes by community type in concentrations of **(a)** total dissolved N (TDN) and **(b)** dissolved organic N (DON), and seasonal changes in **(c)** dissolved inorganic N (DIN), and **(d)** amino acids. Data are mean ± one SE. Same letters above the means indicate nonsignificant differences according to Tukey post-hoc comparison of means tests. There were no significant differences in DIN or amino acid concentrations at the community type x date level (Table 2).

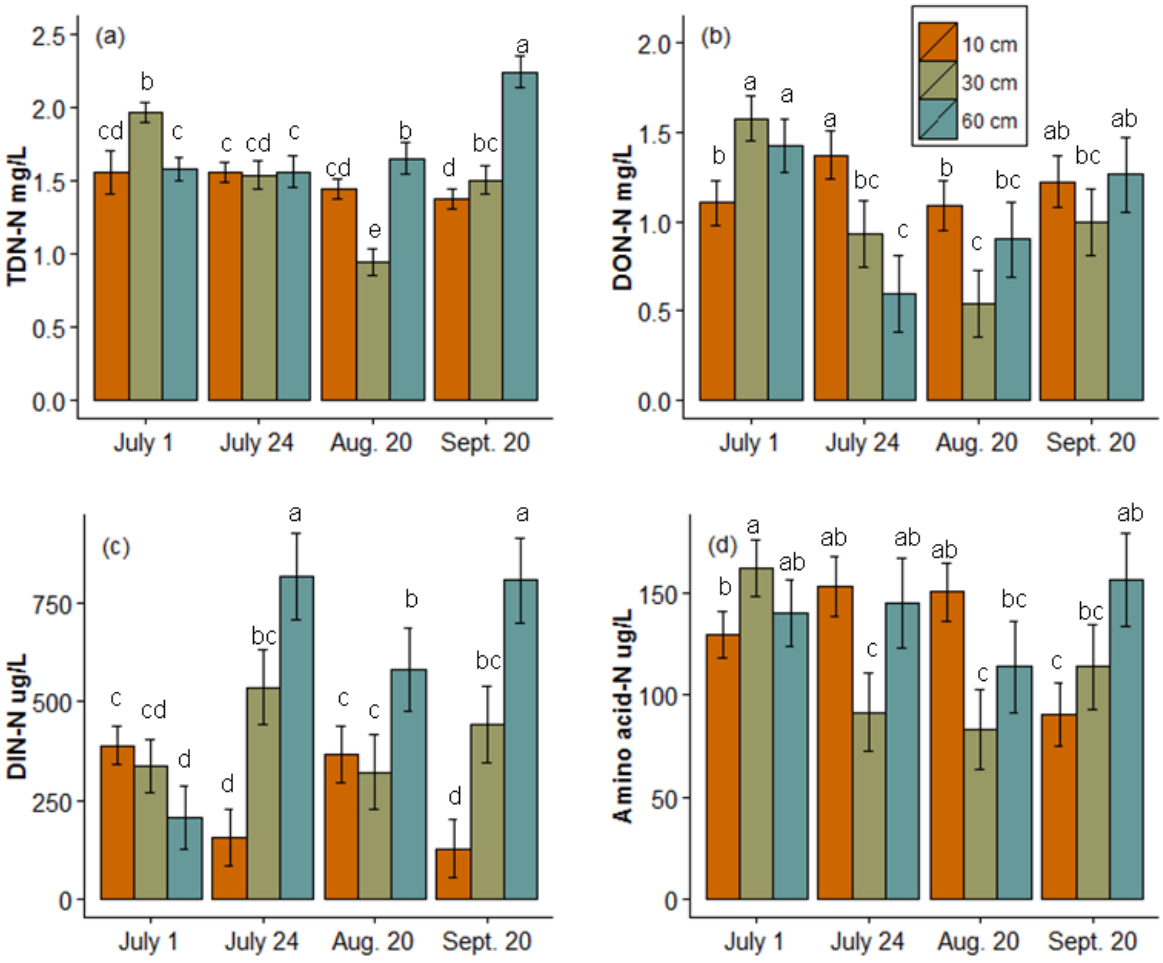

Figure 3.2: Seasonal changes in concentrations of **(a)** total dissolved N, **(b)** dissolved organic N, **(c)** dissolved inorganic N, and **(d)** amino acids by depth. Data are mean ± one SE. Same letters above the means indicate nonsignificant differences according to Tukey post-hoc comparison of means tests.

depth x community type interaction. All community types appeared to have similar concentrations of TDN and DON across depths (Figure). However, DON concentrations in the drunken forest at 30 and 60 cm depths were greater than DON concentrations in the bog at 10 and 60 cm (Figure b). When depth was averaged across community types, I observed the greatest concentrations of TDN and DON in the drunken forest, and the lowest concentrations in the collapse bog. The forested sites (permafrost forest and drunken forest) had the greatest variation and therefore were not significantly different than the other three community types.

Pore water DIN was predominately composed of NH_4^+-N across sampling dates, depths, and locations, with NO_3^--N concentrations at the very low end of analyzer detection limits (mean NO_3^--N approximately 8% of total DIN). There was an observed community type effect on DIN concentrations, with an apparent gradual increase of DIN along the permafrost thaw gradient, with the moat and collapse scar bog having the largest concentrations of DIN (Table 4.2, Figure c). Seasonal DIN pore water data revealed a significant difference in DIN concentrations between sampling dates and depth (Table 4.2, Figure 3.2c). In early July, DIN availability appeared to be largely confined to shallower soils at 10 and 30 cm. As the season progressed, deeper soils started to contribute more to DIN availability. Analysis of community type interactions by depth, did not indicate a significant difference to mean DIN concentrations (Table 4.2).

I used multiple regression modeling to assess the effects of environmental controls (temperature at 10 cm, seasonal ice depth, and soil moisture at 10 cm) and community type on TDN, DON, and DIN concentrations across the season (Table). DON concentrations were best predicted by temperature and community type. DIN was best predicted by community type and seasonal ice depth. Concentrations of DIN were negatively related to ice depth, with increasing concentrations as seasonal ice depth declined. However, these models had low predictive power, as none of the "best fit" (most parsimonious) models explained more than 20% of the total variation in any given N species.

4.2 Plant responses to permafrost thaw and changing N availability

Canonical correspondence analysis demonstrated clear divisions among community types along the thaw gradients (Figure). Also, because CCA is forced to make plot scores a

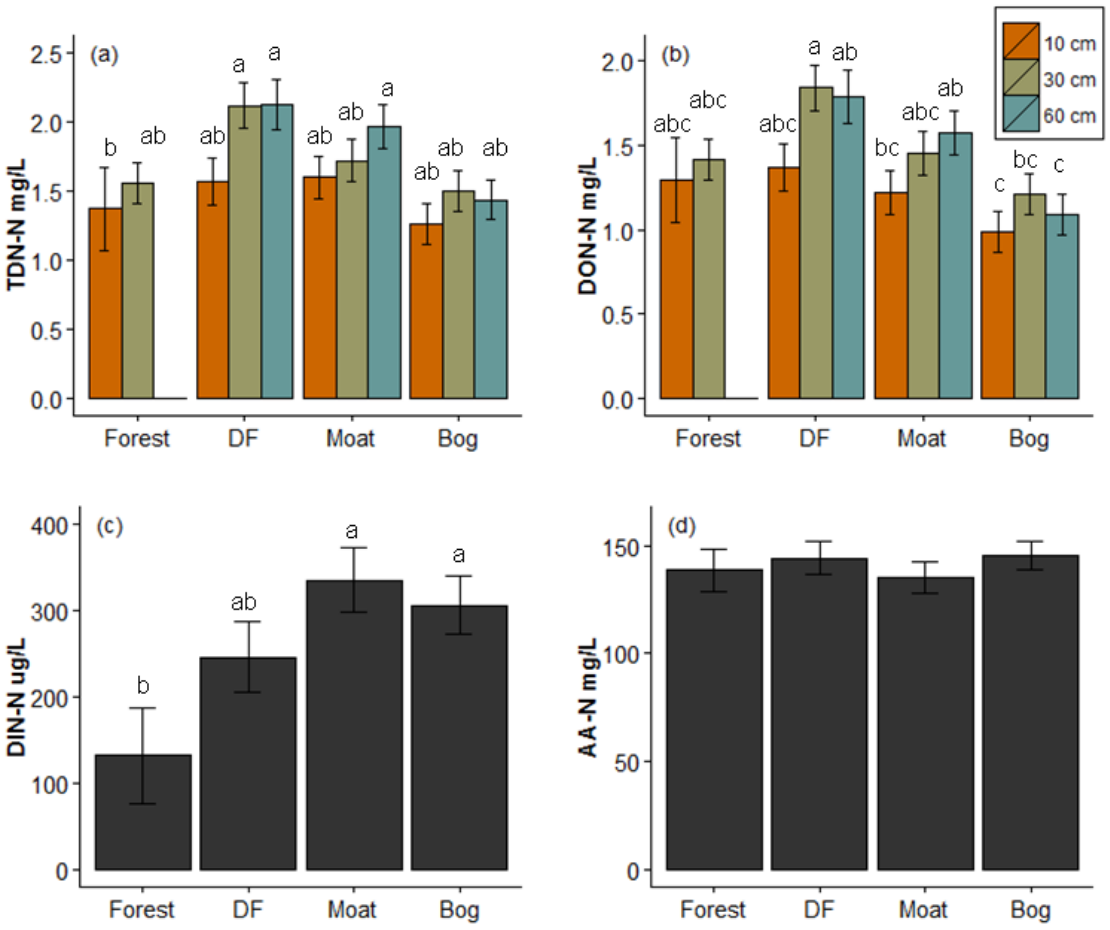

Figure 4.3: Mean concentrations by depth of **(a)** total dissolved N (TDN), and **(b)** dissolved organic N (DON) by depth, and mean concentrations across depths for **(c)** dissolved inorganic N (DIN), and **(d)** amino acids along permafrost thaw gradients comprised a permafrost forest (Forest), drunken forest with active permafrost collapse (DF), moat representing recent permafrost thaw, and collapse scar bog (Bog). Data are mean ± one SE. Same letters above the means indicate nonsignificant differences according to Tukey post-hoc comparison of means tests between community type * depth interactions. There were no significant differences in DIN or amino acid concentrations at the community type * depth level (Table 2).

Table 4.3: Multiple regression best fit models for predicting N pore water availability. Possible explanatory variables included soil temperature at 10 cm (Temp), soil moisture at 10 cm (Moist), and seasonal ice depth (Ice). Potential models were compared using backwards regression and AIC values.

	Terms	Coefficients	*p*	R^2_{adj}	F
TDN			**<.001*** **	**0.084**	**9.247** $_{4,357}$
	(Intercept)	1.669	< .001***		
	Temp	-0.024	0.022*		
	Drunken Forest	0.381	< .001***		
	Forest	-0.020	0.878		
	Moat	0.384	< .001***		
DIN			**<.001*** **	**0.044**	**5.24** $_{4,357}$
	(Intercept)	0.445	< .001***		
	Ice	-0.001	0.046*		
	Drunken Forest	-0.119	0.061		
	Forest	-0.279	< .001***		
	Moat	0.072	0.124		
DON			**<.001*** **	**0.191**	**5.45** $_{15,346}$
	(Intercept)	1.377	< .001***		
	Temp	-0.026	0.003**		
	Drunken Forest	0.418	< .001***		
	Forest	0.158	0.145		
	Moat	0.315	< .001***		

***p<0.001, **p<0.01, *p<0.05

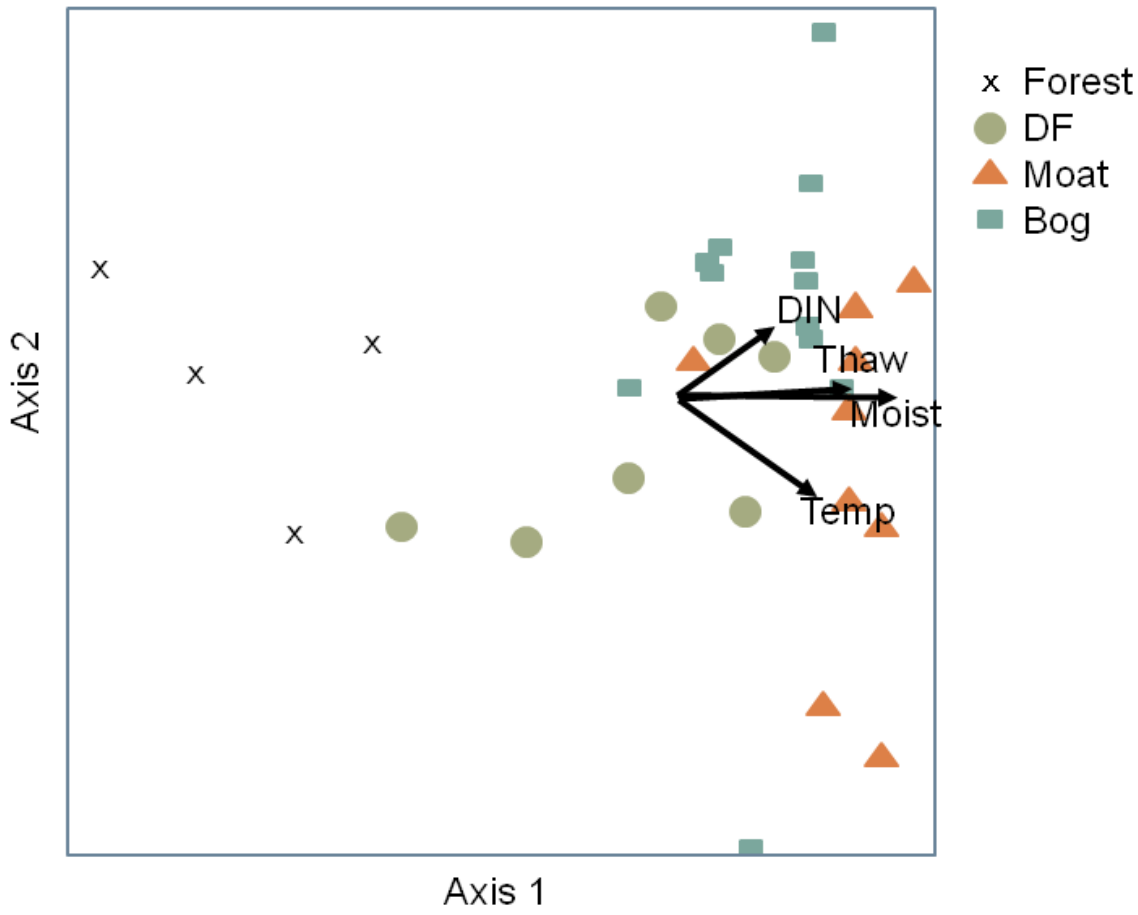

Figure 4.4: Canonical correspondence ordination of plot-level percent cover species data and environmental variables including mean seasonal soil temperature at 10 cm (Temp), mean seasonal soil moisture at 10 cm (Moist), maximum seasonal ice thaw depth (Thaw), mean plot-level TDN, DIN, and DON. Axis 1 explains 17.4 % of residual variability and Axis 2 explains an additional 7.0% for a total of 24.4% of cumulative explain variability. Pearson's correlation between sample scores from the species data and the sample scores from the linear combinations of environmental variables are 0.939 for Axis 1 and 0.701 for Axis 2.

function of the environmental variable data matrix, I can also infer that major environmental variables of ice depth, soil moisture at 10 cm, soil temperature at 10 cm, and mean DIN pore water concentrations are highly correlated to each other and to species distribution across the gradient (Figure). Increases in DIN concentrations appeared to correspond to the clustering of bog sample plots. Variations in seasonal ice depth and soil moisture appeared to be most closely related to each other, while temperature slightly deviated from the other two environmental vectors along Axis 2 (Figure). MRPP results further supported observed trends in CCA ordination, with clear separation between community types (A=0.19, p<0.001). According to both CCA and post-hoc contrast testing following MRPP, permafrost forest plant communities were the most distinct compared to the other gradient community types (p<0.01 for all contrasts). MRPP pairwise comparisons also revealed that drunken forests and moat communities had slight overlap with regards to species composition (A=0.05, p=0.09), but drunken forest plots did not share traits with bog communities (A=0.09, p=0.01). The collapse bog and moat community types also overlap with each other with regards to species composition and ordination space (A=0.02,p=0.18); however, overlap between moat communities and the two adjacent community types (drunken forest and bog) is attributed to ecotonal transitions associated with studying a natural gradient.

Shifts in plant functional group abundances were observed from percent cover estimates (Figure). Forest communities had the greatest number of nonvascular and vascular plant functional groups, and the greatest number of species within each functional group (Table A-1**)**. Bryophyte communities were dominated by both *Sphagnum* and feather moss species, and vascular plant communities largely were dominated by ericaceous evergreen dwarf-shrubs and forbs (mostly *Rubus chamaemorus*). In the thaw communities, I observed large changes in *Sphagnum,* sedge, and evergreen shrub cover. *Sphagnum* cover varied across the community types ($F_{3,38}$= 16.4, p < 0.001), with increases in the drunken forest, moat, and collapse bog relative to the permafrost forest. Sedge cover also increased with thaw ($F_{3,38}$=7.0, p < 0.001), with the greatest abundance of sedges found in the moat relative to the other community types. Conversely, evergreen shrub coverage decreased along the transect ($F_{3,38}$=25.51, p < 0.001), with the lowest percentage of evergreen shrubs found in the moat. Successional development of the collapse scar bogs increased the abundance for both evergreen and deciduous shrubs (mainly

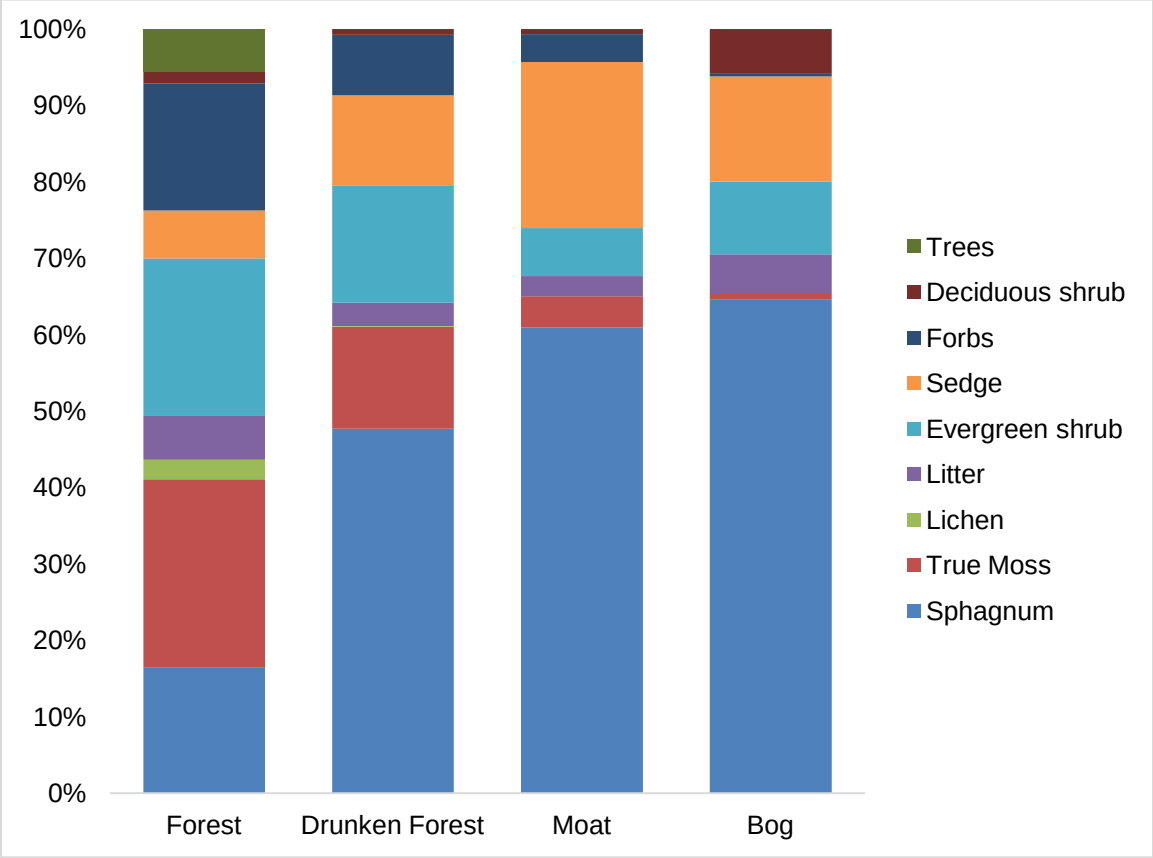

Figure 4.5: Visual estimates of percent cover for subcanopy (<1 m) and ground cover plant species across thaw gradients.

Betula species), while sedges remained an important part of the collapse bog community (Figure).

Multiple regression models were used to examine controls on dominant plant functional groups (evergreen shrubs, deciduous shrubs, sedges, and *Sphagnum*), and species found across three or more community types (*C. calyculata, B. glandulosa*, and *C. aquatilis*). Of the four functional groups selected for model construction, only sedge communities failed to converge with an adequate predictive model based on either N availability or environmental variables (Table 3.4). Evergreen shrub cover was positively related to concentrations of DIN, DON, and mean soil temperature, but was negatively related to concentrations of TDN. To a lesser extent, deciduous shrub cover also was positively related to soil temperature, but was also influenced by seasonal ice depth and DON availability. Environmental variables explained more variation in *Sphagnum* cover and individual species distribution than soil solution N concentrations. *Sphagnum* coverage was largely controlled by changes in soil moisture across the gradient. Both *C. aquatilis* and *C. calyculata* coverage appeared to be controlled by seasonal ice depth, which is unsurprising for *C. aquatilis* because it is only found in areas where permafrost is beginning to thaw (drunken forest) or has completely thawed (moat, bog). Increases in soil temperature corresponded to increased *B. glandulosa* cover, which was the only studied species or functional type to solely be predicted by an environmental variable.

The root abundance varied by a community type x depth interaction ($F_{4,331}$=27.67, p < 0.001). Within the top 30 cm of the soil profile, permafrost forest plants had the greatest root abundance, with maximum relative root abundance increasing significantly with depth (Figure)? Soil cores from the permafrost forest did not extend beyond 35 cm due to the presence of permafrost, which inhibited continued coring. In the drunken forest, there was a nonlinear pattern in rooting density as rooting depths extended into the deeper, unfrozen soils (Figure). In the moat and collapse bog communities, root abundance increased in the upper 60 cm of soil, with the greatest root abundances in the bottom-most section of each core on average. Root abundance indices and foliar N concentrations did not appear to be correlated (Figure).

C. calyculata foliage N concentrations varied by a community type x sampling date interaction ($F_{7,54}$=56.17, p<0.001). Along the gradient, both summertime N and litterfall N percentage increased (summer: $F_{3,27}$=4.383, p =0.012; fall:$F_{3,27}$=5.444, p=0.004). At peak

Table 3.4: Multiple regression best fit models for predicting vegetation percent cover. Possible explanatory variables included mean soil temperature at 10 cm (Temp), mean soil moisture at 10 cm (Moist), mean seasonal ice depth (Ice), mean total dissolved nitrogen (TDN), mean dissolved inorganic nitrogen (DIN), and mean dissolved organic nitrogen (DON). Potential models were compared using backwards regression and AIC values.

	Terms	Coefficients	*p*	R^2_{adj}	F
Evergreen shrubs			**0.005****	**0.263**	**6.35** $_{2,28}$
	(Intercept)	-20.792	0.156		
	DON	21.838	0.004**		
	Temp	2.305	0.053		
Deciduous shrubs			**0.007****	**0.279**	**4.88** $_{3,27}$
	(Intercept)	4.109	0.622		
	DON	-8.169	0.074		
	DIN	18.168	0.033 *		
	Ice	0.072	0.084		
Sedge			**0.202**	**0.023**	**1.70** $_{1,29}$
	(Intercept)	31.050	0.006*		
	Moist	-0.200	0.202		
***Sphagnum* moss**			**<0.001**	**0.429**	**12.26** $_{2,28}$
	(Intercept)	15.893	0.207		
	DON	12.386	0.176		
	Moist	0.845	<.001***		
Chamaedaphne calyculata			**0.011**	**0.223**	**5.32** $_{2,28}$
	(Intercept)	10.033	0.033		
	Ice	-0.139	0.003**		
	Moist	0.233	0.021*		
Betula glandulosa			**0.051**	**0.125**	**4.16** $_{1,29}$
	(Intercept)	-6.684	0.167		
	Temp	1.163	0.051		
Carex aquatilis			**0.008****	**0.219**	**8.15** $_{1,29}$
	(Intercept)	-2.171	0.460		
	Ice	0.065	0.008**		

***p<0.001, **p<0.01, *p<0.05

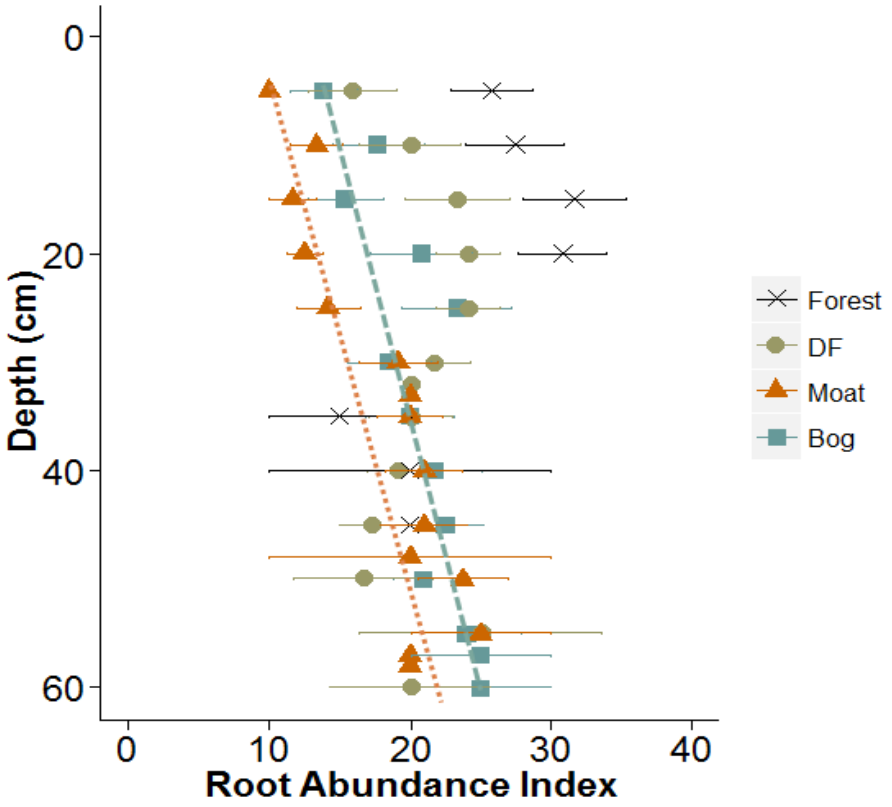

Figure 4.6: Root abundance index value by depth across thaw gradient community types. Moat and bog regressions with depth are shown with dotted lines and are significant at a 95% confidence interval (Moat R^2=0.31, p-value<00.1; Bog R^2=0.12, p-value<0.001).

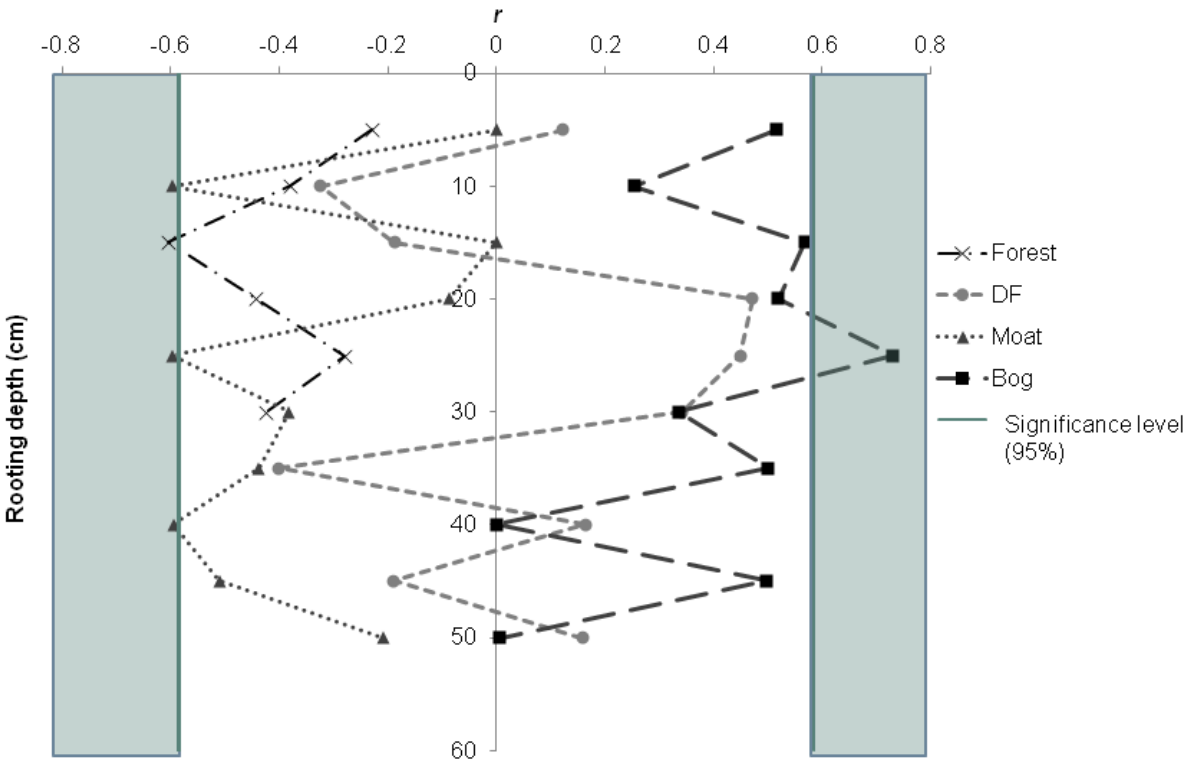

Figure 4.7: Pearson correlations (*r*) of root abundance index values by 5 cm soil increments and mean foliar N across gradient community types (n=9 for all community types.). Green boxes indicate boundaries for correlation significance at the 95 % confidence interval where points found within shaded area have a significance correlation between root abundance index and rooting depth.

biomass, foliar N averaged 1.15% in the permafrost forest, and was significantly lower than the other community types, in which mean foliar N ranged 1.50-1.61%. Bog litterfall was significantly higher than either the thaw ecotone community or the forest and had the highest N percentage at 0.59% N (Figure). Due to corresponding changes in both summertime foliar N concentration and litterfall N concentration, resorption efficiencies were fairly consistent across the gradient and ranged between 0.60-0.70. However, higher levels of N in litterfall did result in slightly decreased RE for bog *C. calyculata* plants ($F_{3,27}$=3.542, p=0.027). Bog community plants had the lowest mean RE at approximately 0.60, but were only statistically lower than plants growing in collapse scar moats.

Mean DIN pore water concentrations were positively related to summertime and litterfall foliage N concentrations (summer: R^2=0.18, p<0.001; litter:R^2=0.38, p<0.001; Figure a,b). However, while there was a slight negative relationship between concentrations of DIN and RE, no significant interaction between DIN and RE was observed (p=0.17; Figure c). No significant relationships between DON or TDN and leaf chemistry were identified.

Stable isotope values varied across the gradient for all three species of interest. Foliage δ^{15}N values for *C. calyculata* and *B. glandulosa* were the most depleted in the forest compared to the other community types (Table 4.4, Figure). Because *C. aquatilis* is an obligate wetland species, no specimens were collected from the drier, wooded permafrost forest. (Figure). Due to a small sample size, no clear trends can be interpreted from drunken forest samples of *B. glandulosa.* However as soils continued to saturate with the formation of the moat and bog, δ^{15}N values became more depleted with collapse scar bog succession (Table 4.4, Figure). Correlations between foliar δ^{15} N and pore water chemistry revealed a slight correlation with DIN (R^2=0.03, p=0.002) and a weak correlations with organic N measurements (R^2=0.02, p=0.051). There was no significant correlation between isotope fractionation and amino acid measurements.

Chapter 5: Discussion

5.1 Overview

One major goal of this study was to examine potential changes in plant-available N along a permafrost-thaw gradient and to assess whether changes could be attributed to surface, active

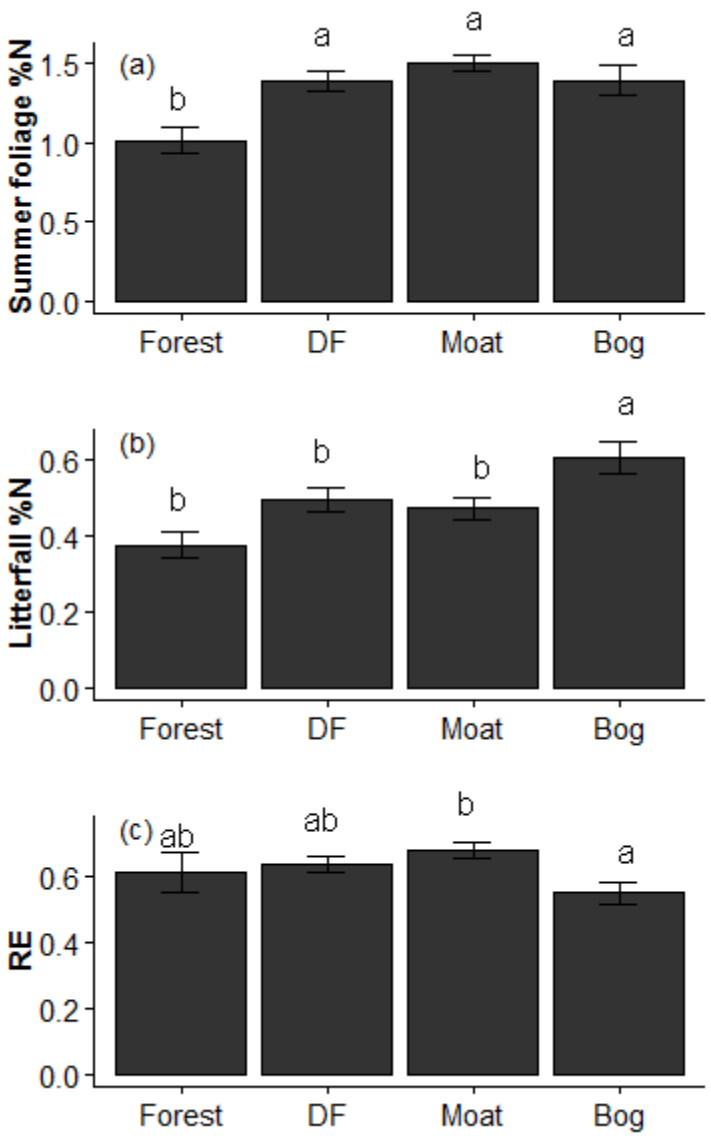

Figure 4.8: Comparison of *C. calyculata* foliage N concentrations (mean±se) from (**a**) peak biomass; and **(b**) senesced foliage collected from litter traps in autumn. Nutrient resorption efficiency (RE) **(c**) has been calculated as the change in summer foliage N and senesced foliage N percentages. Letters indicate post-hoc test differences between community types.

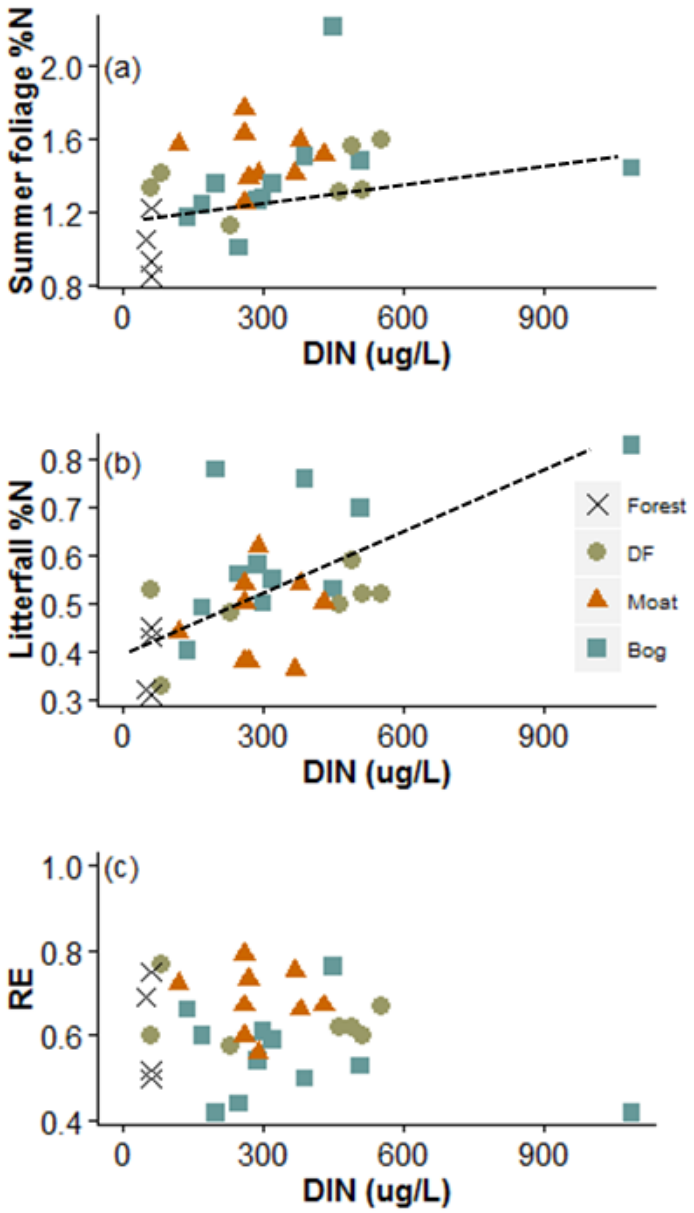

Figure 4.9: Scatter plot of foliage N concentrations in *C. calyculata* versus DIN pore water concentrations for (**a**) summer foliage, (**b**) litterfall, and (**c**) resorption efficiency. Lines indicate significant linear regressions at the 95 % confidence level. Summer foliage vs DIN: R^2=0.153, $F_{(1,29)}$=6.418, p=0.017. Litterfall vs DIN: R^2=0.37, $F_{(1,29)}$=17.9, p<0.001.

Table 4.4: Results from of one-way ANOVA of $\delta^{15}N$ fractionation by community type. Results are listed for all combined species and at the species level. Post-hoc comparisons are between community types: permafrost forest (F), drunken forest (DF), moat (M), and collapse scar bog (B).

	Community Type		
	df	F	Post-hoc
Species	3,78	**11.67*** **	DF,M,B>F
Betula glandulosa	3,10	**4.20***	M>F
Carex aquatilis	2,53	**5.13****	DF>B
Chamaedaphne calyculata	3,59	**14.30*** **	DF>F,B; M>F,B

***p<0.001, **p<0.01, *p<0.05

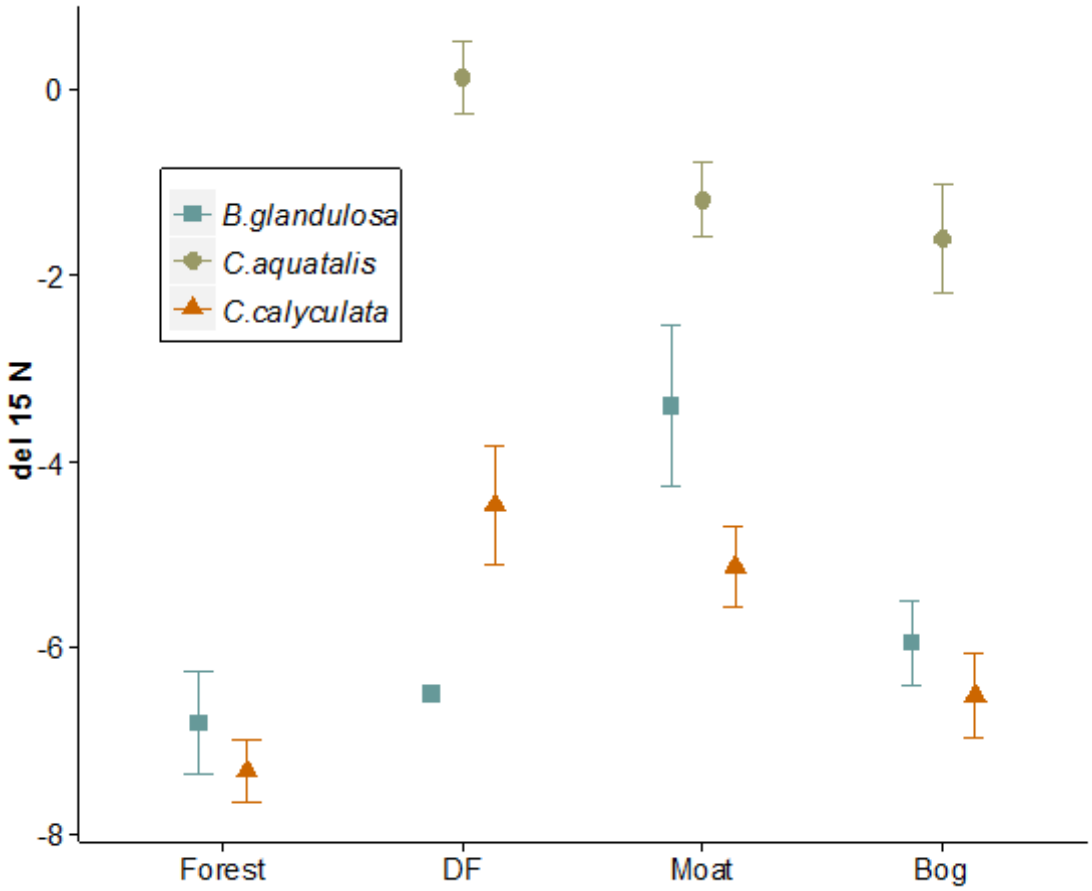

Figure 4.10: Comparison of δ^{15} N fractionation between thermokarst community types for three commonly found species: *Betula glandulosa* (*B. gladulosa*), *Carex aquatalis* (*C. aquatalis*), and *Chamaedaphne calyculata* (*C. calyculata*) (mean value ± se).

layer or deeper thawing permafrost processes. Permafrost thaw is generally expected to cause increases in N availability by augmenting soil N pools and turnover rates. However, increased saturation and low redox conditions in thermokarst wetlands could constrain N mineralization. In general, the results supported several of my predictions. For example, as expected, I found that DIN availability increased following thaw, with the greatest mean DIN concentrations in the moat and collapse scar bog communities. Early in the growing season, higher DIN concentrations were associated with near-surface soils, as N turnover in deeper soils was constrained by the presence of seasonal ice. However, during maximum thaw in September, DIN availability was attributed more to deeper soil horizons for all of the communities impacted by thaw. Several of my predictions regarding changes in N availability post-thaw were not supported by my findings. For example, I had predicted that DIN availability would be highest in the drunken forest where permafrost is actively thawing, but instead found greater concentrations in the moat and collapse scar bog communities. Therefore, the greatest changes in inorganic N availability post thaw appear to be related to longer-term (decades to centuries) successional processes and the potential transfer of DIN and DON from thawing communities into collapse scar bogs.

A second major goal of this thesis was to explore relationships between N availability, plant species abundance, and plant traits related to N uptake and use. To address this goal, I measured species cover, rooting abundance with depth, foliar N concentrations, foliar $\delta^{15}N$ values, and related environmental predictors including depth of seasonal ice/permafrost, and soil moisture and temperature at 10 cm depths. Despite predictions that changes in N availability following thaw would alter plant species distribution, N concentrations were not a strong direct predictor of dominant species or functional group coverage. However DIN availability did appear as a significant vector through canonical correspondence analysis, suggesting that inorganic nitrogen availability may co-occur with post-thaw succession. My predictions regarding relationships between rooting depths and plant foliar chemistry of *Chamaedaphne calyculata* were supported, as I found that foliar summertime and litterfall N concentrations were positively correlated with DIN concentrations across the thaw gradients. Foliar $\delta^{15}N$ of plant leaves also varied along the permafrost-thaw gradients. Together, these results support the conclusion that plants alter rooting strategies and patterns of plant-N uptake in response to

permafrost thaw. These findings are described in more detail below, where I discuss potential environmental and ecological drivers of N availability along this thermokarst gradient, and compare my findings to results from other sub-arctic permafrost thaw systems.

5.2 Is increased N availability due to increased turnover of active layer or permafrost organic matter upon the onset of thaw?

A comparison of results across the permafrost forest and the two community types related to recent thaw (drunken forest and moat) allows for an assessment of how active thaw of permafrost organic matter effects N availability, without the additional complications of longer-term post-thaw succession in the collapse scar bog. As predicted, DIN availability generally increased with thaw, with the greatest mean DIN concentrations in the moat and the lowest concentrations in the permafrost forest (Figure). I used soil solution measurements at different depths to examine whether increases in DIN concentrations were associated more with active layer or with deeper thawing permafrost horizons. Warming of surface, active layer soils following thaw is expected to stimulate mineralization rates and N availability. If increases in DIN concentrations were only observed in near surface soils, this would suggest that increased N turnover in active layer horizons are primarily driving DIN increases. However, thawed permafrost soils have the potential to mobilize large amounts of N (Harden *et al.* 2012), in addition to these active layer dynamics. Therefore if my measurements demonstrated greater DIN concentrations at depth in the communities impacted by thaw, this would support the prediction that N "released" or mobilized from permafrost SOM is driving increases in N availability.

In the drunken forest, where permafrost is actively thawing, seasonal average concentrations of TDN and DON were greater than those measured in the permafrost forest (Figure 4.). Concentrations of DIN averaged across sampling periods and depths, however, did not vary among community types. While my results suggest clear trends in TDN along the thaw gradients driven by the DON pool, trends in DIN concentrations did not show significant increases following thaw. This result conflicts with previous studies that have suggested that large amounts of labile N may be released upon the onset of thaw (Harden *et al.* 2012; Keuper *et al*. 2012). One possible explanation is that permafrost SOM is recalcitrant due to mineralization

processes that occurred in the active layer before the SOM was incorporated into the permafrost table (Coolen *et al.* 2011), resulting in low levels of gross N mineralization. However, another explanation is that because lowland boreal forests are notably N-limited (Aerts 1990; Van Cleve *et al.* 1983), any release of DIN from thawing permafrost SOM may be immediately taken up by soil microorganisms or plants and ultimately lead to decreases in DIN pool sizes and net mineralization. This suggests that instantaneous measurements of pore water may not be sufficient for characterizing N cycling mechanisms.

Along the thaw gradient studied here, the transition from drunken forest to moat communities represents the most dramatic shift in both environmental and vegetative characteristics (Table 4.1). The moat plots were characterized by open, treeless canopies, increased soil temperatures, soil saturation, and the complete absence of near-surface permafrost. As predicted, the moat had the highest mean DIN concentrations, showing a significant increase relative to the drunken forest. Trends in DIN concentrations with depth in the moat were similar to those reported in Figure 3.2, with major inputs of DIN found in both surface and deeper soil depths. This suggests that N mineralization is occurring throughout the rooting profile, resulting in overall greater DIN availability.

Data collected throughout the growing season show that DIN availability is controlled mainly by near-surface soils when seasonal ice is still present, but that deeper soil horizons contribute more to N availability as seasonal ice recedes (Figure 3.2). Later in the growing season, near-surface soil DIN concentrations decrease, likely due to increases in plant and microbial uptake. This suggests that a deepening active layer and warmer soil conditions are the major contributors to plot-level seasonal increases in DIN. Another possible explanation is that the thawing of deep soils accompanied by a rising water table may also deliver deeper nutrient sources into the reach of plants. Additionally, my models did not find any predictive relationship between surface soil temperature and DIN (Table). This further supports the hypothesis that DIN availability is not entirely controlled by N mineralization in near-surface soils, but instead deeper soils may be contributing labile DIN into the system as seasonal ice and permafrost melts. These field observations also support findings of Keuper *et al.* (2012), who used laboratory incubations to conclude that recently thawed soils may increase N availability in boreal lowlands by increasing unfrozen soil N pools and mineralization processes.

Previous research has suggested that permafrost thaw can release large stocks of potentially labile dissolved organic matter (Frey & McClelland 2009; Gorham 1991; Grosse *et al.* 2011; Jones *et al.* 2012). It is reasonable to assume that this would also include the mineralization of simpler, monomeric organic N molecules that would be readily available to both plants and microbes. In my study, DON is likely serving as an important substrate for N mineralization as microbes become less N limited thus leading to increases in thermokarst pore water NH_4^+ concentrations (Aerts & Chapin 2000; Keuper *et al*. 2012; Updegraff *et al.* 1995). My data suggest that DON mineralization was a key determinant of DIN concentrations; in August an increase in DIN availability was observed, coupled with a corresponding decrease in DON (Figure 3.2). This suggests that increased microbial mineralization activity is occurring during late-summer when soil temperatures are at their warmest. While it is possible that DON is leached downward from active layer soils and with ecological succession and the transition from drunken forest, to moat, to collapse scar bog (Currie *et al.* 1996; Hedin *et al.* 1995), any leached DON would likely be highly recalcitrant and not readily available for microbial mineralization as smaller, more labile nutrients would have likely already been taken up by plants or microbes (Frey & McClelland 2009; Neff *et al.* 2003). Therefore, thawing permafrost SOM may be the most readily available DON source driving increased mineralization with depth and warming along the thaw gradient.

Despite increases in pore water DON upon the onset of thaw, plant-available DON may not be altered by thaw. Studies of mosses (Kielland 1997; Krab *et al.* 2008) and northern sedges and ericaceous shrubs (Aerts & Chapin 2000; Chapin *et al.* 1993; Kielland 1994) have indicated that these functional groups may be well adapted to utilize DON as a direct nitrogen supply. However, only monomers, such as amino acids, are readily available for plant uptake (Chapin *et al.* 1993; McFarland *et al.* 2010; Werdin-Pfisterer *et al.* 2009). Larger organic N molecules may be too large to permeate through cell membranes, and require depolymerization, or symbiotic mycorrhizal partnership before they can be taken up by plants (Schimel & Bennett 2004). I used concentrations of amino acids as a measure of plant-available DON, but my results show no significant changes in amino acid concentrations along the thaw gradient or at varying depths (Figure). However amino acids concentrations did steadily decline throughout the growing season with smallest concentrations found in September (Figure 4.). This appears to be opposite

to trends in DON concentrations, suggesting that more recalcitrant compounds dominate pore water DON.

5.3 How does long-term ecosystem succession following thaw alter N cycling dynamics?

Transitions between forested (permafrost forest and drunken forest) and thermokarst (moat and collapse scar bog) community types are marked by drastic shifts in environmental conditions along with shifts in vegetation and soil characteristics involved in post-thaw succession. Because collapse scar peat vertically accumulated above the water table for several hundred years following thaw, my deepest sampling points (60 cm) were no longer in direct contact with permafrost SOM, but instead consisted entirely of SOM that had accumulated post-thaw. Comparing trends in N availability in the collapse scar bogs relative to the permafrost forest or the earlier stages of permafrost thaw thus allows for an assessment of how aspects of N cycling change during post-thaw succession. In general, I observed greater DIN concentrations in the collapse scar bog compared to the permafrost forest, though concentrations were lower than in the moat (Figure). Additionally on a volumetric basis, there might be lot more N available in bog community types compared to forested sites because of much deeper aquatic profiles. As collapse scar bogs develop, N availability may begin to decline over time following thaw, given that soil conditions become relatively drier, colder, and more acidic as peat accumulates further from the water table.

Similar to patterns observed in the moat, increased mineralization of DON, as opposed to direct release of DIN from thawing permafrost, seems like the most plausible mechanism of increasing DIN concentrations in the collapse bog. Increased N mineralization rates in the bog are also likely to be driven by environmental conditions (warmer soils upon thawing) and accumulating SOM. However, despite increases in DIN availability, collapse scar bogs may impose limitations to plant N uptake as soils become saturated and anoxic. As permafrost thaws, plant communities that were once limited by impenetrable, frozen soils now must address issues involving oxygen transport. Saturated soil conditions can create a “soil barrier-N limitation” (Vitousek *et al.* 2010), as the abundance of water can severely interfere with plant root metabolism and respiration due to root oxygen deficiencies (Reddy & DeLaune, 2008). Furthermore, because the collapse scar bogs in this system are completely surrounded by

permafrost peat plateaus, these wetlands are ombrotrophic (Vitt *et al.* 1994) which further limits oxygen and nutrient transport. Therefore a simple increase in pore water DIN concentrations may not directly result in greater plant-N uptake, so other metrics must be used to quantify changes to plant-N uptake and use.

Key environmental variables such as soil moisture, temperature, and seasonal ice depth did not account for much of the variation in pore water N concentrations (Table). This likely is at least partly methodological, as I used environmental data from 10 cm depth as predictors of mean pore water N concentrations, yet clearly soil conditions vary in the soil profile with depth. Because data suggest that deeper soils are contributing to changes in N availability, deep soil temperature and moisture may have more accurately predicted changes in TDN. However, other environmental controls that I did not quantify, such as changes in pH and redox potential, and gross mineralization and microbial uptake, may be influencing N dynamics along these thaw gradients (Updegraff *et al.* 1995). Changes in soil bulk density may also influence N availability and plant uptake (Bridgham *et al.* 2001), both as permafrost initially begins to thaw in the forest, and as peat accumulates post-thaw in collapse scar bogs.

5.4 How are plants responding to changes in N economies upon thaw?

As permafrost begins to thaw, vegetation shifts from an ericaceous shrub understory that is restricted by a shallow active layer, cold soils, and low moisture availability, to a wetland community that is adapted to warmer soils and saturated, potentially anaerobic conditions. In northern wetlands systems, faster growing species, such as sedges and deciduous shrubs, are found in sites with warmer and wetter soil conditions (Jorgenson *et al*. 2013), deeper rooting profiles (Kohzu *et al.* 2003), and greater soil nitrogen availability (Myers-Smith *et al.* 2008). Slower-growing species such as ericaceous shrubs are excluded from wetland communities post-thaw (Karlsson *et al.* 1987). I found that total root abundance increased with depth following permafrost thaw, which could be associated increased uptake of nutrients mobilized from thawing permafrost organic matter. Though not examined in my study, deeper rooting species, especially sedges, often have belowground aerenchymous tissue that would assist with nutrient uptake under anoxic conditions (Cronk & Fennessy 2001; Rydin & Jeglum 2006). My results show that the bulk of roots found at depth were classified as fine and very fine roots (data not

shown), indicating that plants may be modifying root architecture in order to increase nutrient acquisition strategies by investing in faster growing, deeper penetrating roots, (Jackson *et al.* 2008). Because these finer roots have high N, low C:N, short lifespans and often rapid decomposition rates (Pregitzer 2002; Ruess *et al.* 2003), a high root biomass at depth likely contributes to high microbial activity – linking a feedback cycle between deeper SOM decomposition and plant nutrient uptake.

Canonical correlation analysis of plant species cover and distribution showed that DIN concentrations were a significant environmental vector in separating most of the bog and moat sites from the forested study plots (Figure). However, contrary to my predictions, DIN concentrations had little predictive power with regards to cover of functional group and individual plant species. Deciduous shrub cover was the only plant group related to variation in DIN concentration, which explained approximately 20% of the total variation in shrub cover. Instead, my results suggest that changing soil conditions along the gradients, such as increasing soil temperature, soil moisture, and seasonal ice depths, played a larger role in dictating shrub and sedge species abundance and distribution (Figure , Table 3.4).

Understanding whether deeper roots directly or indirectly participated in the mobilization of N from permafrost OM was beyond the scope of this study. However, I was able to explore whether increased investment of deep roots was correlated with higher foliar N concentration, which could serve as evidence that shifts in root depth distribution and growth with thaw increased plant N uptake. Root abundance indices in surface or deeper soil layers were not correlated with foliar N concentration (Figure). One possible explanation is that aspects of the rhizosphere such as rooting profiles have little impact on foliar N, which might be expected in systems with very conservative N recycling. Alternatively, increased plant N uptake at depth may not actually translate into greater foliar N concentrations if plants respond to increasing nutrient availability by increasing belowground and/or aboveground productivity, which could lead to relative constant foliar C/N despite accelerated nutrient uptake. Faster growing species, such as sedges and deciduous shrubs, will increase uptake under increased nutrient availability and increase net primary production (NPP; Chapin 1980) compared to evergreen shrubs that store additional nutrients in tissues. Another potential explanation for the lack of relationships

between DIN availability and foliar N concentrations is that plants may be outcompeted by microbes for available N in soil.

Previous research in arctic tundra and northern forests has linked rooting depth and changing N soil availability with variations in foliar $\delta^{15}N$ values (Garten 1993; Nadelhoffer *et al*. 1996; Robertson *et al.* 1999). Observed variation in ^{15}N enrichment in thermokarst ecotonal transition zones of the drunken forest and moat suggests that plant species may receive nutrients from different sources, depths or through different mechanisms along the thaw gradient. Nadelhoffer *et al.* (1996) compared $\delta^{15}N$ values of sedges and ericaceous shrubs in the Arctic, and found relationships between more enriched $\delta^{15}N$ values in sedge species and deeper rooting profiles. In contrast, more depleted $\delta^{15}N$ values were measured in plants that relied primarily on nutrients from shallower, near surface soils and are often associated with mycorrhizae. These findings are consistent with my results, where *C. aquatalis*, a deep rooting plant, generally had more enriched $\delta^{15}N$ values than either of the two tested shrub species (Figure). Additionally, as root abundance increased at depth in the drunken forest, both shrub species experienced foliar $\delta^{15}N$ enrichment. However, all three species had more depleted foliar $\delta^{15}N$ values in the bog compared to the other community types, which conflicts with my prediction that deeper rooting would correspond to higher $\delta^{15}N$ values. Instead, changes in N source and availability may be responsible for the observed variation in $\delta^{15}N$ values across the thaw gradients. On average along the gradients with thaw, I observed a slight positive correlation between $\delta^{15}N$ values and DIN availability, possibly due to discrimination against ^{15}N during mineralization (Nadelhoffer *et al*. 1996). However, observed fractionation during N mineralization likely occurs during nitrification, and not ammonification (Hogberg 1997; Kahmen *et al.* 2008), yet NO_3^- availability appeared to be very low in pore water solutions collected from this study. One possible explanation for this phenomenon is that gross nitrification is taking place, but $NO_3^-$is immediately taken up by biological activity and is therefore not measured from collections of soil pore water (Stark & Hart 1997). Therefore, if N fractionation during mineralization is driving changes in foliar $\delta^{15}N$ signatures, further investigation of gross nitrification rates along lowland boreal thaw gradients would need to be conducted. Changes in mycorrhizal ecology may also be impacting $\delta^{15}N$ values. Generally, plants with mycorrhizal associations have more depleted plant signatures relative to N sources due to substrate fractionation by the fungal partner

(Asada *et al.* 2005; Evans, 2001; Sorrell *et al.* 2011). Conversely, non-mycorrhizal plants can become slightly ^{15}N enriched as NH_4^+ increases due to microbial preferences for light isotopes, resulting in $\delta^{15}N$ enrichment with peat depth (Asada *et al*. 2005; Kohzu *et al*. 2003). Part of the observed changes in isotopic enrichment from this study may be due to altered mycorrhizal associations as soils saturate. Both *B. glandulosa* and *C. calyculata* have known mycorrhizal associations (ectomycorrhiza and ericoid, respectively) in northern systems (Hobbie *et al*. 2009; Inselsbacher & Näsholm 2012; Read *et al.* 2004). However, soil saturation may disrupt rhizome fungal communities (Muthukumar *et al.* 2004). Plant foliage from the forest is likely more depleted than adjacent saturated community types because permafrost thaw may displace mycorrhizal networks as soil moisture increases and saturates in ecotonal communities, thereby leading to enrichment in ^{15}N. Over successional time, collapse scar bogs develop hummock-hollow topography that may allow mycorrhizae to reinvade the roots of ericaceous shrubs as the developing hummocks provide a sanctuary for hyphae above the water table, and $\delta^{15}N$ values approached those from foliage collected in the forest.

Found in all four community types along the thaw gradients, *C. calyculata* is an evergreen plant known to store additional nutrients as simple organic compounds within plant tissues (Bartsch 1994, Bubier *et al.* 2011). Therefore I used this species as a "model plant" or indicator of whether changes in N availability translated into altered plant N uptake or use, given that it is ubiquitous both before and following permafrost thaw. My results based on this species support my prediction that N-availability is increasing and that plants are utilizing this N, as I found increasing N concentrations in *C. calyculata* summertime foliage and litterfall that were correlated with increasing DIN availability. Despite changes in foliage chemistry, I only observed a slight reduction in resorption efficiency in the bog, indicating that N availability may not significantly exceed the N demands of vegetation in collapse scar bogs. Further investigation of collapse scar bog nutrient dynamics, including a more complete understanding of nitrogen and phosphorus limitations to productivity, may be needed to better understand whether collapse bog vegetation remains N limited, or whether increases in N availability following thaw shift these systems to become more limited by P. My data on N:P in foliage from dominant species along the thaw gradients had mean values ranging from 6.5-15.6 (Figure 1.2), suggesting that most of

these plants remain N limited (N:P<13.5) or N and P co-limited (13.5≤N:P≤16; Güsewell & Koerselman 2002) post thaw.

In addition to vascular plant growth, increased N supplies can also lead to greater *Sphagnum* production, and thus peat accumulation rates. Several other studies have observed increases in peat accumulation following permafrost thaw that authors in general have attributed to increases in NPP post-thaw (Camill *et al.* 2001; Turetsky *et al.* 2007)**.** However, no studies to my knowledge have identified whether these increases in peat accumulation rates could be due at least in part to supplemental nitrogen supplies post-thaw. In a greenhouse study, Granath *et al.* (2012) found that certain, faster-growing species of *Sphagnum* (like *S. riparium*, which is common in moat and collapse bog communities), increase production in response to small increases in nitrogen supplies. While a long-term fertilization experiment would be a more direct test of how increasing N (and P) supplies influence vegetation productivity and peat accumulation rates, this does suggest that the increases in N concentration observed in the first part of my study likely are sufficient for triggering increased productivity in at least some dominant collapse bog plants.

Chapter 6: Conclusions

This study found that plant-available N concentrations increase in boreal lowlands following permafrost thaw. Two major drivers appear to be contributing to these increases in N availability: 1) SOM released from thawing permafrost organic matter in areas of active thaw, particularly late in the growing season when thaw is deepest, and 2) warmer soil conditions during later stages of post-thaw succession that stimulate microbial activity and N mineralization in both near-surface and deeper soils. Saturating soil conditions, increased active layer depth, and warmer soil temperatures also altered plant species composition, causing community changes from ericaceous shrubs in the lowland permafrost forest towards more hydrophilic vegetation functional types including sedges and *Sphagnum* in the moat and collapse scar bog. While changes in organic or inorganic N concentrations did not appear to serve as direct drivers of plant species change, increases in N availability did appear to alter plant N use strategies by increasing

rooting depth profiles, increasing foliar nitrogen concentrations, altering $\delta^{15}N$ values, and potentially shifting the mycorrhizal associations of dominant plants.

Recent research in Alaska has shown widespread permafrost thaw throughout the discontinuous permafrost zone, especially in fine-grained and poorly drained lowlands similar to my study area (Camill & Clark, 1998; Jorgenson *et al*. 2013, Jorgenson *et al.* 2001). My results demonstrated that short-term inputs from permafrost SOM may increase organic N supplies on decades to century time scales, but that longer term trends in ecosystem succession post-thaw is likely to increase plant-available N over much longer time periods. The changes in plant-available N and plant N traits observed in this study also could have major implications for peat accumulation rates and decomposition processes. If changes in nutrient availability post thaw increase productivity and peat accumulation rates, this could serve to partially offset observed and predicted permafrost C release (Grosse *et al*. 2011; Harden *et al*. 2012; Zimov *et al.* 2006). Currently there is ongoing debate about whether post-thaw increases in peat accumulation might outweigh deep soil C losses (Jones *et al.* 2012), or whether deep soil C losses exceeded increases in post-thaw peat accumulation rates (O'Donnell *et al*. 2011). Therefore how plants and microbes respond to changes in post-permafrost thaw N availability will likely play a large role in the relative carbon balance between inputs and losses associated with permafrost thaw.

Chapter 7: References

Aerts, R. (1990). Nutrient use efficiency in evergreen and deciduous species from heathlands. *Oecologia*, *84*, 391–397.

Aerts, R. (1996). Nutrient resorption from senescing leaves of perennials: are there general patterns? *Journal of Ecology*, *84*, 587–608.

Aerts, R., & Chapin, F. S. I. (2000). The mineral nutrition of wild plants revisited: a re-evaluation of processes and patterns. *Advances in Ecological Research*, *30*, 1–67.

Aerts, R., Verhoeven, J. T. A., & Whigham, D. F. (1999). Plant-mediated controls on nutrient cycling in temperate fens and bogs. *Ecology*, *80*(7), 2170–2181.

Asada, T., Warner, B. G., & Aravena, R. (2005). Nitrogen isotope signature variability in plant species from open peatland. *Aquatic Botany*, *82*(4), 297–307. doi:10.1016/j.aquabot.2005.05.005

Bartsch, I. (1994). Effects of fertilization on growth and nutrient use by Chamadaphne calyculata in a raised bog. *Canadian Journal of Botany*, *72*, 323–329.

Beilman, D. W. (2001). Plant community and diversity change due to localized permafrost dynamics in bogs of western Canada. *Canadian Journal of Botany*, *79*(8), 983–993.

Berendse, F., & Aerts, R. (1987). Nitrogen-use efficiency: A biologically meaningful definition. *Functional Ecology*, *1*(3), 293–296.

Bolker, B. M., Brooks, M. E., Clark, C. J., Geange, S. W., Poulsen, J. R., Stevens, M. H. H., & White, J.-S. S. (2009). Generalized linear mixed models: a practical guide for ecology and evolution. *Trends in Ecology & Evolution*, *24*(3), 127–35. doi:10.1016/j.tree.2008.10.008

Bridgham, S. D., Updegraff, K., & Pastor, J. (2001). A Comparison of Nutrient Availability Indices Along an Ombrotrophic – Minerotrophic Gradient in Minnesota Wetlands. *Soil Science Society of America Journal*, *65*, 259–269.

Bubier, J. L., Smith, R., Juutinen, S., Moore, T. R., Minocha, R., Long, S., & Minocha, S. (2011). Effects of nutrient addition on leaf chemistry, morphology, and photosynthetic capacity of three bog shrubs. *Oecologia*, *167*(2), 355–68. doi:10.1007/s00442-011-1998-9

Camill, P. (1999). Patterns of boreal permafrost peatland vegetation across environmental gradients sensitive to climate warming. *Canadian Journal of Botany*, (77), 721–733.

Camill, P. (2005). Permafrost thaw accelerates in boreal peatlands during late-20th century climate warming. *Climate Change*, *68*, 135–152.

Camill, P., & Clark, J. S. (1998). Climate change disequilibrium of boreal permafrost peatlands caused by local processes. *American Natualist*, *151*(3), 207–222.

Camill, P., Lynch, J. A., Clark, J. S., Adams, J. B., & Jordan, B. (2001). Changes in biomass, aboveground net primary production, and peat accumulation following permafrost thaw in the boreal peatlands of Manitoba, Canada. *Ecosystems*, *4*(5), 461–478.

Chapin, F. S. I. (1980). The mineral nutrition of wild plants. *Ann*, *11*, 233–260.

Chapin, F. S. I., Moilanen, L., & Kielland, K. (1993). Preferential use of organic nitrogen for growth by a non-myc. *Nature*, *361*(6401), 150–153.

Chapin, F. S., McGuire, A. D., Ruess, R. W., Hollingsworth, T. N., Mack, M. C., Johnstone, J. F., … Taylor, D. L. (2010). Resilience of Alaska's boreal forest to climatic change. *Canadian Journal of Forest Research*, *40*(7), 1360–1370.

Churchill, A. (2011). The response of plant community structure and productivity to changes in hydrology in Alaskan boreal peatlands. M.S. thesis, University of Alaska Fairbanks.

Coolen, M. J. L., van de Giessen, J., Zhu, E. Y., & Wuchter, C. (2011). Bioavailability of soil organic matter and microbial community dynamics upon permafrost thaw. *Environmental Microbiology*, *13*(8), 2299–314. doi:10.1111/j.1462-2920.2011.02489.x

Cronk, J. K., & Fennessy, M. S. (2001). *Wetland plants: biology and ecology* (p. 439).

Currie, W. S., Aber, J. D., Mcdowell, W. H., Boone, R. D., & Magill, A. H. (1996). Vertical transport of dissolved organic C and N under long-term N amendments in pine and hardwood forests. *Biogeochemistry*, *35*(3), 471–505.

Euskirchen, E. S., Edgar, C. W., Turetsky, M. R., Waldrop, M. P., & Harden, J. W. (2014). Differential response of carbon fluxes to climate in three peatland ecosystems that vary in the presence and stability of permafrost. *Journal of Geophysical Research*, *119*, 1576–1595. doi:10.1002/2014JG002683.Received

Evans, R. D. (2001). Physiological mechanisms influencing plant nitrogen isotope composition. *Trends in Plant Science*, *6*(3), 121–6. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/11239611

Frey, K. E., & McClelland, J. W. (2009). Impacts of permafrost degradation on arctic river biogeochemistry. *Hydrological Processes*, *23*(1), 169–182. doi:10.1002/hyp.7196

Garten, C. T. (1993). Variation in foliar 15N abundance and the availability of soil nitrogen on Walker Branch Watershed. *Ecology*, *74*(7), 2098–2113.

Gorham, E. (1991). Northern peatlands: role in the carbon cycle and probable response to climatic warming. *Ecological Applications*, *1*(2), 182–195.

Granath, G., Strengbom, J., & Rydin, H. (2010). Rapid ecosystem shifts in peatlands: linking plant physiology and succession. *Ecology*, *91*(10), 3047–56. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/21058564

Granath, G., Strengbom, J., & Rydin, H. (2012). Direct physiological effects of nitrogen on Sphagnum: a greenhouse experiment. *Functional Ecology*, *26*(2), 353–364.

Grosse, G., Harden, J., Turetsky, M., McGuire, a. D., Camill, P., Tarnocai, C., … Striegl, R. G. (2011). Vulnerability of high-latitude soil organic carbon in North America to disturbance. *Journal of Geophysical Research*, *116*, 1–23. doi:10.1029/2010JG001507

Güsewell, S., & Koerselman, W. (2002). Variation in nitrogen and phosphorus concentrations of wetland plants. *Perspectives in Plant Ecology, Evolution and Systematcis*, *5*, 37–61.

Harden, J. W., Koven, C. D., Ping, C.-L., Hugelius, G., David McGuire, a., Camill, P., … Grosse, G. (2012). Field information links permafrost carbon to physical vulnerabilities of thawing. *Geophysical Research Letters*, *39*(15), n/a–n/a. doi:10.1029/2012GL051958

Harris, S. A., French, H. M., Heginbottom, J. A., Johnston, G. H., Ladanyi, B., Sego, D. C., & Everdingen, R. O. Van. (1988). Glossary of permafrost and related ground-ice terms. *National Research Council of Canada*, (142).

Hedin, L. O., Armesto, J. J., & Johnson, A. H. (1995). Patterns of nutrient loss from unpolluted , old-growth temperate forests : evaluation of biogeochemical theory. *Ecology*, *76*(2), 493–509.

Hobbie, J. E., & Hobbie, E. a. (2006). 15N in symbiotic fungi and plants estimates nitrogen and carbon flux rates in Arctic tundra. *Ecology*, 87(4), 816–822.

Hobbie, J. E., Hobbie, E. a, Drossman, H., Conte, M., Weber, J. C., Shamhart, J., & Weinrobe, M. (2009). Mycorrhizal fungi supply nitrogen to host plants in Arctic tundra and boreal forests: 15N is the key signal. *Canadian Journal of Microbiology*, *55*(1), 84–94. doi:10.1139/W08-127

Hogberg, P. (1997). Tansley Review No . 95 15 N natural abundance in soil-plant systems. *New Phytologist*, *137*, 179–203.

Hothorn, T., Bretz, F., & Westfall, P. (2008). Simultaneous inference in general parametric models. *Biometrical Journal*, *50*(3), 346–363.

Inselsbacher, E., & Näsholm, T. (2012). The below-ground perspective of forest plants: soil provides mainly organic nitrogen for plants and mycorrhizal fungi. *The New Phytologist*, *195*(2), 329–34. doi:10.1111/j.1469-8137.2012.04169.x

Jackson, L. E., Burger, M., & Cavagnaro, T. R. (2008). Roots, nitrogen transformations, and ecosystem services. *Annual Review of Plant Biology*, *59*, 341–63. doi:10.1146/annurev.arplant.59.032607.092932

Jones, D. L., & Kielland, K. (2002). Soil amino acid turnover dominates the nitrogen flux in permafrost-dominated taiga forest soils. *Soil Biology and Biochemistry*, *34*, 209–219.

Jones, J. B. (2005). Nitrogen loss from watersheds of interior Alaska underlain with discontinuous permafrost. *Geophysical Research Letters*, *32*(2), 1–4. doi:10.1029/2004GL021734

Jones, M. C., Booth, R. K., Yu, Z., & Ferry, P. (2012). A 2200-year record of permafrost dynamics and carbon cycling in a collapse-scar bog, interior Alaska. *Ecosystems*, *16*(1), 1–19. doi:10.1007/s10021-012-9592-5

Jorgenson, M. T., Harden, J., Kanevskiy, M., O'Donnell, J., Wickland, K., Ewing, S., … Koch, J. (2013). Reorganization of vegetation, hydrology and soil carbon after permafrost degradation across heterogeneous boreal landscapes. *Environmental Research Letters*, *8*(3), 035017. doi:10.1088/1748-9326/8/3/035017

Jorgenson, M. T., Racine, C. H., Walters, J. C., & Osterkamp, T. E. (2001). Permafrost degradation and ecological changes associated with a warming climate in central alaska. *Climate Change*, *48*(4), 551–579.

Kahmen, A., Wanek, W., & Buchmann, N. (2008). Foliar delta(15)N values characterize soil N cycling and reflect nitrate or ammonium preference of plants along a temperate grassland gradient. *Oecologia*, *156*(4), 861–70. doi:10.1007/s00442-008-1028-8

Karlsson, P. S. (1987). Micro-site performance of evergreen and deciduous dwarf shrubs in a subarctic heath in relation to nitrogen status. *Holarctic Ecology*, *10*(2), 114–119.

Keuper, F., Bodegom, P. M., Dorrepaal, E., Weedon, J. T., Hal, J., Logtestijn, R. S. P., & Aerts, R. (2012). A frozen feast: thawing permafrost increases plant-available nitrogen in subarctic peatlands. *Global Change Biology*, *18*, 1998–2007.

Kielland, K. (1994). Amino acid absorption by arctic plants : implications for plant nutrition and nitrogen cycling. *Ecology*, *75*(8), 2373–2383.

Kielland, K. (1997). Role of free amino acids in the nitrogen economy of actic Cryptogams. *Ecoscience*, *4*(1), 75–79.

Kielland, K., McFarland, J. W., Ruess, R. W., & Olson, K. (2007). Rapid Cycling of Organic Nitrogen in Taiga Forest Ecosystems. *Ecosystems*, *10*(3), 360–368. doi:10.1007/s10021-007-9037-8

Klapstein, S. J., Turetsky, M. R., McGuire, A. D., Harden, J. W., Czimczik, C. I., Xu, X., … Waddington, J. M. (2014). Controls on methane released through ebullition in peatlands affected by permafrost degradation. *Journal of Geophysical Research: Biogeosciences*, *119*, 418–431. doi:10.1002/2013JG002441.Received

Kohzu, A., Matsui, K., Yamada, T., & Sugimoto, A. (2003). Significance of rooting depth in mire plants : Evidence from natural 15 N abundance. *Ecological Research*, *18*, 257–266.

Krab, E. J., Cornelissen, J. H. C., Lang, S. I., & Logtestijn, R. S. P. (2008). Amino acid uptake among wide-ranging moss species may contribute to their strong position in higher-latitude ecosystems. *Plant and Soil*, *304*(1-2), 199–208. doi:10.1007/s11104-008-9540-5

Kruskal, J., & Wish, M. (1978). *Multidemensional scaling*. Sage Publications, Newbury Park, California.

McCune, B., & Mefford, M. (1999). PC-ORD-Multivarate analysis of ecological data, version 4 edition. MjM Software Design, Gleneden Beach, Oregon.

McFarland, J. W., Ruess, R. W., Kielland, K., Pregitzer, K., Hendrick, R., & Allen, M. (2010). Cross-ecosystem comparisons of in situ plant uptake of amino acid-N and NH4 +. *Ecosystems*, *13*(2), 177–193. doi:10.1007/s10021-009-9309-6

Muthukumar, T., Udaiyan, K., & Shanmughavel, P. (2004). Mycorrhiza in sedges--an overview. *Mycorrhiza*, *14*(2), 65–77. doi:10.1007/s00572-004-0296-3

Myers-Smith, I. H., Harden, J. W., Wilmking, M., Fuller, C. C., McGuire, A. D., & Chapin, F. S. I. (2008). Wetland succession in a permafrost collapse : interactions between fire and thermokarst. *Biogeosciences*, *5*, 1273–1286.

Nadelhoffer, K. J., Shaver, G. R., Fry, B., Giblin, A., Johnson, L., & McKane, R. (1996). 15N natural abundances and N use by tundra plants. *Oecologia*, *107*, 386–394.

Nasholm, T., Ekbald, A., Nordin, A., Giesler, R., Hogberg, M., & Hogberg, P. (1998). Boreal forest plants take up organic nitrogen. *Nature*, *392*(30 April), 914–916.

Natali, S. M., Schuur, E. a. G., & Rubin, R. L. (2012). Increased plant productivity in Alaskan tundra as a result of experimental warming of soil and permafrost. *Journal of Ecology*, *100*(2), 488–498. doi:10.1111/j.1365-2745.2011.01925.x

Neff, J. C., Chapin, F. S. I., & Vitousek, P. M. (2003). Breaks in the cycle : dissolved organic nitrogen in terrestrial ecosystems in a nutshell : *Frontiers in Ecology and the Environment*, *1*, 205–211.

O'Donnell, J. A., Jorgenson, M. T., Harden, J. W., McGuire, A. D., Kanevskiy, M. Z., & Wickland, K. P. (2011). The effects of permafrost thaw on soil hydrologic, thermal, and carbon dynamics in an Alaskan peatland. *Ecosystems*, *15*(2), 213–229. doi:10.1007/s10021-011-9504-0

Osterkamp, T. E., Jorgenson, M. T., Schuur, E. A. G., Shur, Y. L., Kanevskiy, M. Z., & Vogel, J. G. (2009). Physical and ecological changes associated with warming permafrost and thermokarst in interior Alaska. *Permafrost and Periglacial Processes*, *256*, 235–256.

Osterkamp, T. E., Viereck, L., Shur, Y., Jorgenson, M. T., Racine, C., Doyle, A., & Boone, R. D. (2000). Observations of thermokarst and its impact on boreal rorests in Alaska. *Arctic, Antarctic, and Alpine Research*, *32*(3), 303–315.

Pinheiro, J., Bates, D., DebRoy, S., Sarakar, D., & Team, R. C. (2014). nlme: Linear and nonlinear mixed effects models.

Pregitzer, K. S. (2002). Fine roots of trees – a new perspective. *New Phytologist*, *154*, 267–273.

Quinton, W. L., & Baltzer, J. L. (2012). The active-layer hydrology of a peat plateau with thawing permafrost (Scotty Creek, Canada). *Hydrogeology Journal*, *21*(1), 201–220. doi:10.1007/s10040-012-0935-2

Read, D. J., Leake, J. R., & Perez-moreno, J. (2004). Mycorrhizal fungi as drivers of ecosystem processes in heathland and boreal forest biomes 1. *Canadian Journal of Botany*, *82*, 1243–1263. doi:10.1139/B04-123

Reddy, K. R., & DeLaune, R. D. (2008). *Biogeochemistry of wetlands*. Taylor and Francis group, Boca Raton, Florida.

Robertson, G. P., Wedin, D., Groffman, P. M., Blair, J. M., Holland, E. A., Nadelhoffer, K. J., & Harris, D. (1999). Soil carbon and nitrogen availability: nitrogen mineralization, nitrification and soil respiration potentials. *Standard soil methods for long-term ecological research* (eds. G.P. Robertson, D.C. Coleman, C.S. Bledsoe, and P. Sollins), pp. 258–271. Oxford University Press, Oxford.

Rosen, H. (1957). A modified ninhydrin colorimetric analysis for amino acids. *Archives of Biochemistry and Biophysics*, *67*(1), 10–15.

Ruess, R. W., Hendrick, R. L., Burton, A. J., Pregitzer, K. S., Sveinbjornsson, B., Allen, M. F., & Maurer, G. E. (2003). Coupling fine root dynamics with ecosystem carbon cycling in black spruce forests of interior Alaska. *Ecological Monographs*, *73*(April 2002), 643–662.

Rydin, H., & Jeglum, J. K. (2006). *The biology of peatlands 2nd edition*. Oxford University Press, Oxford.

Schimel, J. P., & Bennett, J. (2004). Nitrogen mineralization: challenges of a changing paradigm. *Ecology*, *85*(3), 591–602.

Schurr, E. A. G., Crummer, K. G., Vogel, J. G., & Mack, M. C. (2007). Plant species composition and productivity following permafrost thaw and thermokarst in Alaska tundra. *Ecosystems*, *10*(2), 280–292.

Sorrell, B. K., Chagué-Goff, C., Basher, L. M., & Partridge, T. R. (2011). N:P ratios, δ15N fractionation and nutrient resorption along a nitrogen to phosphorus limitation gradient in an oligotrophic wetland complex. *Aquatic Botany*, *94*(2), 93–101. doi:10.1016/j.aquabot.2010.11.006

Stark, J. M., & Hart, S. C. (1997). High rates of nitrification and nitrate turnover in undistrubed coniferous forests. *Nature*, *385*, 61–64.

Turetsky, M. R., Wieder, R. K., Vitt, D. H., Evans, R. J., & Scott, K. D. (2007). The disappearance of relict permafrost in boreal north America: Effects on peatland carbon storage and fluxes. *Global Change Biology*, *13*(9), 1922–1934.

Updegraff, K., Pastor, J., Bridgham, S. D., & Johnston, C. A. (1995). Environmental and Substrate Controls over Carbon and Nitrogen Mineralization in Northern Wetlands. *Ecological Applications*, *5*(1), 151–163.

Van Cleve, K., Barney, R., & Schlentner, R. (1981). Evidence of temperature control of production and nutrient cycling in two interior Alaska black spruce ecosystems. *Canadian Journal of Forest Research*, *11*, 258–273.

Van Cleve, K., Oliver, L., Schlentner, R., Viereck, L. A., & Dyrness, C. (1983). Productiviey and nutrient cycling in taiga forest ecosystems. *Canadian Journal of Forest Research*, *13*, 747–766.

Vitousek, P. M., Porder, S., Houlton, B. Z., & Chadwick, O. a. (2010). Terrestrial phosphorus limitation: mechanisms, implications, and nitrogen-phosphorus interactions. *Ecological Applications*, *20*(1), 5–15. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/20349827

Vitt, D. H., Halsey, L. A., & Zoltai, S. C. (1994). The bog landforms of continental western Canada in relation to climate and permafrost patterns. *Arctic and Alpine Research*, *26*(1), 1–13.

Weedon, J., Kowalchuk, G., Aerts, R., van Hal, J., van Logtestijn, R., Neslihan, T., … van Bodegom, P. (2012). Summer warming accelerates sub-arctic peatland nitrogen cycling without changing enzyme pools or microbial community structure. *Global Change Biology*, *18*(1), 138–150. doi:10.1111/j.1365-2486.2011.02548.x

Werdin-Pfisterer, N. R., Kielland, K., & Boone, R. D. (2009). Soil amino acid composition across a boreal forest successional sequence. *Soil Biology and Biochemistry, 41*(6), 1210–1220. doi:10.1016/j.soilbio.2009.03.001

Whitledge, T., Malloy, S., Patton, C., & Wirick, C. (1981). *Automated nutrient analysis in seawater*. Brookhaven National Laboratory Technical Report BNZ-51398.

Zimov, S. A., Schuur, E. A. G., & Chapin, F. S. I. (2006). Permafrost and the global carbon budget. *Science, 312,* 1612–1613.

Zoltai, S. C. (1993). Cyclic developments of permafrost in the peatlands of northwestern Alberta, Canada. *Artic and Alpine Research, 25*(3), 240–246.

Zuur, A. F., Ieno, E. N., Walker, N. J., Saveliev, A. A., & Smith, G. M. (2009). *Mixed effects models and extensions in ecology with R*. Springer, New York, New York.

Appendix

Table A-1: List of observed species in designated plant functional groups. Nomenclature from the USDA PLANTS database.

Vascular plant functional group	Species
Evergreen shrubs	*Andromea polifolia, Chamaedaphne calyculata, Oxycoccus microcarpus, Rhododendron groenlandicum, Rhododendron tomentosum, Vaccinium vitis-idaea,*
Trees	*Picea mariana, Larix laricina*
Deciduous shrubs	*Betula gladulosa, Salix bebbiana, Salix pedicellari, Vaccinium uliginosum,*
Sedges	*Carex aquatilis, Carex chordorrhiza, Eriophorum scheuchzeri, Eriophorum vaginatum*
Grasses	*Calamagrostis canadensis*
Forbs	*Comarum palustre, Equisetum arvense, Pedicularis labradorica, Pyrola secunda,*
Other	*Drosera rotundifolia, fungi*

Non-vascular plant functional group	Species
Sphagnum spp.	*Sphagnum angustifolium, Sphagnum capillifolium, Sphagnum fuscum, Sphagnum majus, Sphagnum magellanicum, Sphagnum riparium*
True mosses	*Aulicomnium palustre, Calliergon stramineum, Pleurozium schreberi, Polytrichum strictum*
Lichen	*Caladonia spp., Peltigera aphthosa,*